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Arne Ivar Kvistad

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NTNU
Norwegian University of Science and Technology
Faculty of Natural Sciences and Technology
Department of Biology

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Why Do Some Areas Have Higher Density of Forest Grouse Than Others?

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Arne Ivar Kvistad

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Supervisor: Eivin Røskaft, IBI

Norwegian University of Science and Technology
Department of Biology

Preface

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This thesis is to be regarded as part of the Grouse Management Project 2006 – 2011, the aim of which is to develop science-based, sustainable and economically profitable management practices for the grouse species in Norway (Pedersen et al., 2007). The small game resources are currently not optimally managed and utilised, and there is considerable potential to increase the added value of the grouse harvest. Interdisciplinary research will provide a basis for designing and selecting management models that are better adapted to the terrains, the species' populations, types of land use, and the concerns of landowners.

The research portion of the grouse management project is a collaborative effort between the Norwegian Institute for Nature Research (NINA) and the university colleges of Hedmark (HiHM) and Nord-Trøndelag (HiNT). The project was planned with 2 - 3 master's students included, who are to graduate in June 2011. As the author is an avid hunter with interest in contributing to improved management practices, the project is well-suited in this respect. Since the grouse management project aims to develop a science-based, future-oriented and sustainable management practice, this form a significant part of my motivation to contribute to this work. The results of this thesis may be useful for preparing the handbook of grouse management, which is the project's ultimate goal.

The research community at NINA and at HiNT has got extensive experience in research on grouse species, and has provided useful guidance in my work on this thesis through participation in the grouse management project. In that context, I want to mention I conducted my bachelor's thesis on willow ptarmigan (*Lagopus lagopus*) at HiNT, studying the relationship between the number of grazing sheep (*Ovis aries*) and presence of ptarmigan in a given area. My positive experiences and results from this work have further contributed to my motivation in pursuing this line of study.

Trondheim, 15th of May 2011

Arne Ivar Kvistad

Abstract

In this study landscape characteristics and other components assumed to affect the density of black grouse (*Tetrao tetrix*) and capercaillie (*Tetrao urogallus*) populations have been analysed. Landscape-, predator- and management variables that best explained differences in forest grouse density between relevant study sites in south of Norway have been identified by modelling. The analysis was based upon population densities estimated from forest grouse censuses performed annually in August by the distance sampling method. Density estimates from the period 2004 – 2010 in 19 management areas were utilised.

Geographical Information System was used for extraction of landscape data from available digital maps, and predator- and management data were collected from landowners, research institutions and hunting associations. Linear mixed effect models were used in the modelling process for identification of variables affecting the forest grouse density.

The analysis revealed a positive effect on the black grouse density in spruce-dominated forest (*Picea* spp.) by increased landscape heterogeneity, i.e., a diverse landscape dominated by spruce. In pine-dominated forest (*Pinus* spp.), the results are uncertain due to few observations in this type of forest; however, with the available samples, an increased diversity indicated a negative effect on the black grouse density.

For the capercaillie, the proportions of forest cover and blueberry forest (*Vaccinium* spp.) in an area were proven to affect the density of the species. The analysis indicated, however, that the direction of the density effect was dependent on the forest cover. In areas of low forest cover, the capercaillie density increased when the proportion of blueberry forest increased, while it was opposite in areas of high forest cover.

The density of power lines was identified as a factor affecting the black grouse density negatively. Finally, a positive relationship between pine marten (*Martes martes*) and capercaillie was identified.

Sammendrag

Dette studiet har analysert landskapets egenskaper og dets komponenter som antas å påvirke populasjonstettheten av orrfugl- (*Tetrao tetrix*) og storfugl (*Tetrao urogallus*). Landskaps-, predator- og forvaltningsvariabler som best kan forklare forskjeller i tetthet av skogsfugl mellom relevante studieområder i Sør-Norge har blitt identifisert ved bruk av modellering. Analysene er basert på populasjonstettheter estimert fra årlige takseringer av skogsfugl gjennomført i august måned ved bruk av Distance-metoden. Tetthetsestimater fra perioden 2004 – 2010 i totalt 19 forvaltningsområder har blitt brukt i analysen.

Geografisk informasjonssystem har blitt brukt for å ekstrahere landskapsdata fra tilgjengelige digitaliserte kart, og videre har predator- og forvaltningsdata blitt innsamlet fra grunneiere, forskningsinstitusjoner og jaktforeninger. LME-modeller (Linear Mixed Effect) har blitt brukt i prosessen for å identifisere variabler som påvirker tettheten av skogsfugl.

Analysene påviste en positiv effekt på tettheten av orrfugl i skogsområder dominert av gran (*Picea* spp.) ved et økende mangfold av landskapstyper, dvs. mangfold i et landskap dominert av granskog. I furudominert skog (*Pinus* spp.) er resultatene usikker pågrunn av for få observasjoner i denne skogtypen, men med det gitte datautvalget så indikerte et økt mangfold i landskapet en tendens til negativ påvirkning av orrfugltettheten.

Videre ble det påvist at andelene av skogdekke og blåbærskog (*Vaccinium* spp.) i et område, påvirker tettheten av storfugl. Imidlertid viste retningen av tetthetseffekten å være avhengig av områdets skogdekke. Når andelen av blåbærskog økte, så økte storfugltettheten i områder med lavt skogdekke, mens det var motsatt i områder med høyt skogdekke.

Tettheten av kraftlinjer ble identifisert som en faktor som påvirker orrfugltettheten negativt. Tilslutt ble det påvist en positiv sammenheng mellom tetthetene av mår (*Martes martes*) og storfugl.

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1 Introduction

The Grouse Management Project 2006 – 2011 is a collaborative effort between Statskog and NORSKOG, which represent the largest landowners in public and private sector in Norway, respectively (Pedersen et al., 2007). As part of this project, the landscape characteristics and components assumed to affect the reproduction and density of the grouse species are being analysed, along with possible correlations between density and reproduction. Thus, the following objective, stated by the grouse management project, is central to this thesis: *Identify man-made and natural characteristics at landscape level decisive for habitat quality for ptarmigan / grouse*. The statement encompasses the forest grouse species of this study.

The population density of forest grouse tends to vary a lot both temporary and spatially (Kvasnes et al., 2010). Temporal fluctuations are high for the tetraonidae of Fennoscandia in general; however, for the species of this study, the black grouse (*Tetrao tetrix*) and the capercaillie (*Tetrao urogallus*), the yearly fluctuations are not as strikingly as they are for the ptarmigan (genus *Lagopus*) (Solvang et al., 2007, Solvang et al., 2009).

1.1 Species Status and Habitat Requirements

The grouse populations in Fennoscandia are in decline as a result of habitat degradation (Lande, 2011b) and, possibly, climate change and forestry (Gregersen and Gregersen, 2009); however, the recent decline in forest grouse populations has not been as obvious as observed for the ptarmigan in Norway. This observation is illustrated by the harvesting numbers in Norway during the last two decades (Figure 1). Although hunting statistics do not show population densities precisely, they do reflect population trends. The stock of black grouse is apparently decreasing relatively more than the capercaillie stock, but the hunting bag increased for both species at the end of the last decade. In contrast, ptarmigan populations display no such increase.

In other parts of Europe, the condition of the grouse populations is more serious; both the black grouse and the capercaillie have faced serious decline in Finland in the recent decades (Kurki et al., 2000). These species are locally vulnerable and threatened in parts of central Europe and the UK (Ludwig et al., 2009, Barnes, 1987). The global status of both species, however, is listed as “least concern” by IUCN (IUCN, 2010).

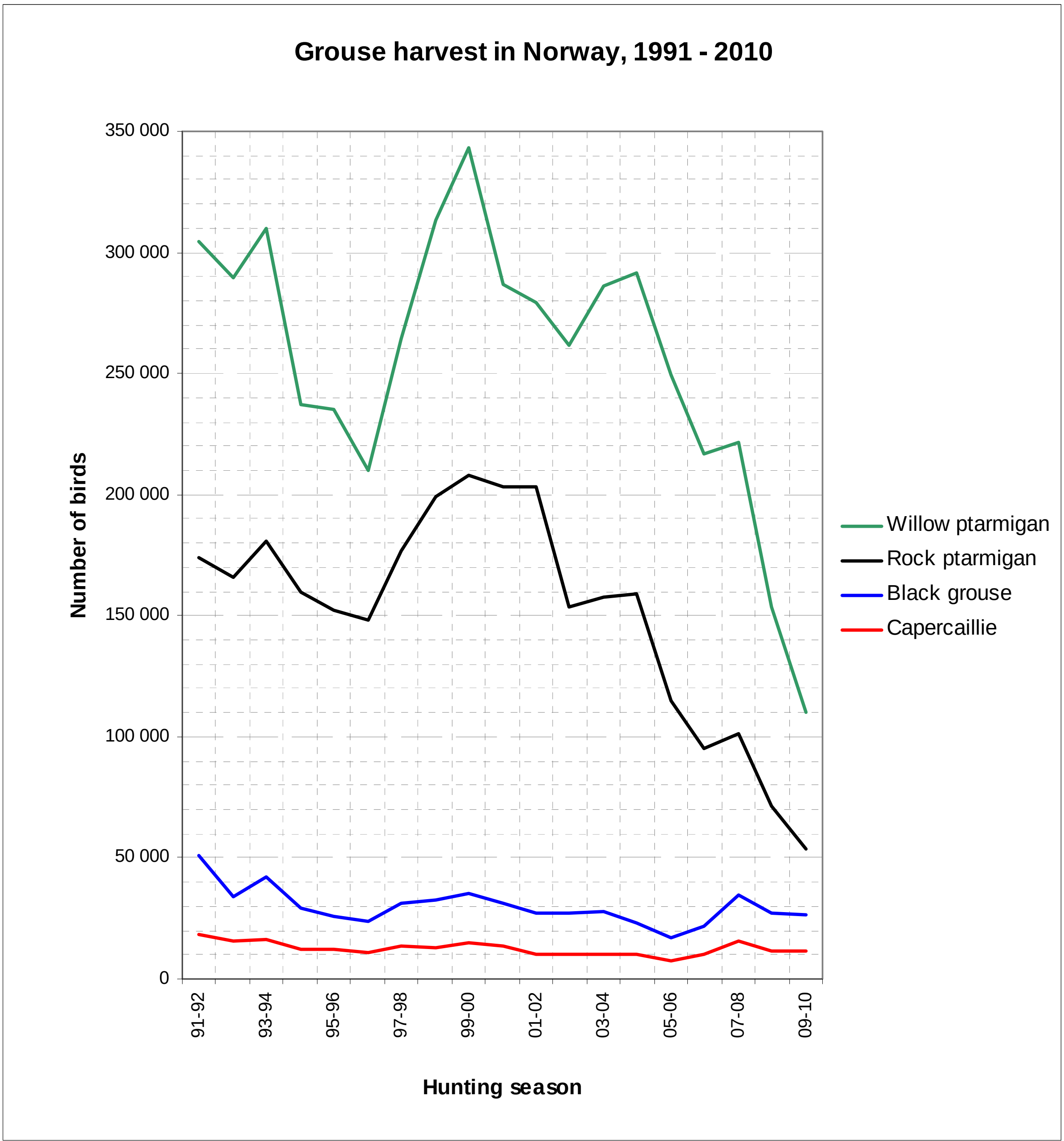

Figure 1. Grouse harvest in Norway, 1991 – 2010 (SSB, 2011).

1.2 Factors Assumed to Influence the Forest Grouse Densities

Whether an area is considered a good habitat for the birds depends on various habitat characteristics and whether these characteristics are suitable to the species in question; however, stochastic events may also have a major influence on the grouse population in a given area. Especially when the populations of forest grouse are low, chick numbers may be severely affected by, for example, a breeding pair of red foxes (*Vulpes vulpes*) or weasels (*Mustela erminea*) settles in the area (Wegge and Kastdalen, 2007, Kurki et al., 1998). In some areas, a relatively large regular population of adult birds may survive the winter, resulting in many broods and a dense population during the subsequent spring. High densities, however, have often been explained by good breeding conditions that result in large broods.

Both the black grouse and the capercaillie belong to the boreal coniferous forests, but they prefer areas in different stages of natural succession (Seiskari, 1962, Swenson and Angelstam, 1993). The capercaillie is associated with the large, continuous boreal forest and prefers the areas in late succession, with older conifer forest. This species is found throughout Norway and is widespread across the Eurasian coniferous forest belt. Unlike the ptarmigan, which are circumpolar distributed, both black grouse and capercaillie are absent from North America. The black grouse is closely associated with the earliest stage of succession in coniferous forest and in general prefers a more open landscape admixed with bogs and open moorland. In contrast to the capercaillie, the black grouse is largely absent from the northernmost region of Norway, i.e., Finnmark county (Hjeljord, 2008, SSB, 2011).

The preferred food sources of the two species are quite different. In winter, both feed in top of trees, but the capercaillie prefers twigs from pine (*Pinus* spp.), or possibly spruce (*Picea* spp.) when the food is scarce. The winter diet of the black grouse consists principally of birch catkins (*Betula* spp.) and juniper (*Juniperus* spp.); however, during winters with less snow, the black grouse may also eat largely from blueberry bushes (*Vaccinium* spp.). In summer, the diet of both species is more similar. All types of berry are important to both species, especially blueberry (Selås, 2000). Sprout, leafs, flowers, cotton grass buds (*Eriophorum* spp.), herbs and ferns are sources of food from early spring through late fall (Hjeljord, 2008).

The chicks eat insects and larvae (Baines et al., 1996, Wegge and Kastdalen, 2008), including mosquitoes and small beetles, which are usually abundant in bog areas and swamp forests. Hence, after the nesting period, which may occur in different type of habitats, broods of both species move to more humid areas nearby (Hjeljord, 2008). Grouse in general tend to move in late summer to habitats in older forest with well-developed blueberry shrubs. Capercaillie broods in particular are associated with forest dominated by blueberry, whereas black grouse tend to prefer more open habitats, like pine bog forest, which have less blueberry cover (Wegge and Kastdalen, 2008).

Human activity may interfere heavily with the quality of forest grouse habitats, e.g., by recreational disturbance (Warren et al., 2009, Thiel et al., 2008) or establishment of infrastructure elements like power lines (Bevanger, 1995), roads and cabins (Taugbøl, 2001). Logging or change of land use, e.g., for agricultural purposes, may cause rapid changes in landscape structures. These changes may even cause permanent loss of habitats, not only for grouse, but for many species (Gregersen and Gregersen, 2009, Kurki et al., 2000).

Predators are known to be important factors of the population dynamics in many small game species, including forest grouse (Angelstam et al., 1984). Boreal landscapes fragmented by human activities may be a cause of elevated predation from generalist predators, especially the red fox, on ground-nestling birds like forest grouse species (Rolstad, 1989). In Finland, abundance of red fox (*Vulpes vulpes*) was shown to increase proportionally with access to young forest and agricultural land (Kurki et al., 1998). In contrast, the pine marten (*Martes martes*) was shown to decrease its abundance in agricultural dominated land and fragmented forest; however, according to Kurki et al. (1998), both pine martens and red fox responded positively to an increased share of young forest in the landscape. The pine marten is usually associated with continuous and dense coniferous forest, which is dominated by large spruce (Brainerd and Rolstad, 2002). Predation by pine martens was proven to be a major factor in capercaillie chicks mortality in a study by Wegge and Kastdalen (2007). In addition, this study found that the goshawk (*Accipiter gentilis*) is also an important predator to capercaillie chicks. Forest grouse serves as an important food source for goshawk, and any strategy for conservation of forest grouse will thus serve as a good conservation strategy for goshawk (Selås et al., 2008). Hagen (1952) has documented that forest grouse is an important pray species for the golden eagle (*Aquila chrysaetos*), which is an indicator species of Norway's terrestrial ecosystems monitoring program (TOV) (Framstad, 2010). Gjershaug and Nygård (2003) refer to several studies that name grouse as one of the golden eagle's preferred prey species in the nesting period.

It is well known that population fluctuations in many small game species correlates with the population fluctuations of small rodents. This correlation is found in grouse populations, though it is not as pronounced in forest grouse species as in ptarmigans (Wegge and Storaas, 1990, Hornfeldt et al., 1986). Small rodents are, however, clearly not a food source for forest grouse and consequently are not a direct cause of the fluctuations in these populations. In a year with small populations of rodents the predators seek alternative food sources. The forest grouse species, including their eggs and chicks, may then serve as the main food source for generalist predators, like crows, foxes and several birds of prey. The next year, the rodents may be much more abundant, and the predators may switch back to their preferred source of food, decreasing predator pressure on the grouse species and facilitating a possible population recovery. This switching, which depends on the relative abundance of prey species, is known as the classical alternative prey hypothesis (Hagen, 1952, Angelstam et al., 1984).

Unlike big game hunting, small game hunting has been subject to occasional and divergent management practice, and is characterized by 1) a mix of private and public landowners and community-owned common land, which has often resulted in minimal coordination between areas; 2) an "established truth" among hunters and landowners that hunters harvest from a production surplus; 3) a management practice based more on long experience than on science. It is a goal of the grouse management project to reform this unscientific practice. In this context, is should be noted that willow ptarmigan populations have been proven to show weak compensation of harvest (Pedersen et al., 2004, Sandercock et al., 2011), which is contradictory to the traditional opinion among hunters. It is likely that this applies to the forest grouse populations as well, but this hypothesis has yet to be proven. Kastdalen (1992) recommended that the harvest rate of an estimated forest grouse population should not exceed 10% at a production rate of 1.4 chicks per female bird.

It is also important to investigate how other management choices affect grouse populations. A good management practice is dependent upon several factors. Firstly, the areas should be large enough to hold stocks undergoing normal population dynamic processes. Data on dispersal ability in tetraonid species indicate that a management unit should be of a certain minimum size to account for the effect of migration to and from surrounding areas. Considering the effects of predator species on the production and density of the birds, a management entity should be significantly larger than the current average size (Brainerd et al., 2005). Secondly, different hunting regulations, e.g., to control the forest grouse harvest, may influence survival and production of chicks the next year (Kastdalen, 1992, Pedersen et al., 2004). Thirdly, protection mechanisms, like the establishment of refuges or the preservation of female birds in a certain area or during a specified timeframe, may protect a population of forest grouse from depletion or even help to re-establish a viable population (Willebrand and Hornell, 2001, Hörnell-Willebrand, 2005).

This thesis is based on estimates of black grouse and capercaillie densities (Chapter 2.2) in Norway. It is desired by the grouse management project to investigate variations in the population numbers collected by these surveys in relation to parameters such as regulations, harvesting rates, small rodents, predator pressure, habitat and vegetation types, and human accessibility and disturbance from roads, power lines, cabins, and settlement in these areas.

1.3 Thesis Objective and Problem Definition

Main objective to address:

Identify and investigate available landscape-, predator- and management variables that best explain differences in forest grouse density between relevant study sites in Norway.

This study is based on the population densities in hunting areas, as estimated from censuses performed annually in August by distance sampling (Buckland and Anderson, 2001). In this study, modelling is used to identify factors affecting the species density at a range of study sites. As a consequence, predictions are not appropriate at this stage. The interpretation of the results is based on a definition of the best-classified forest grouse habitats as those areas that are regularly found to have the highest population densities.

2 Methods and Materials

2.1 Study Areas

The study areas used in this thesis are mainly located in three different regions in south Norway as depicted in Figure 2.

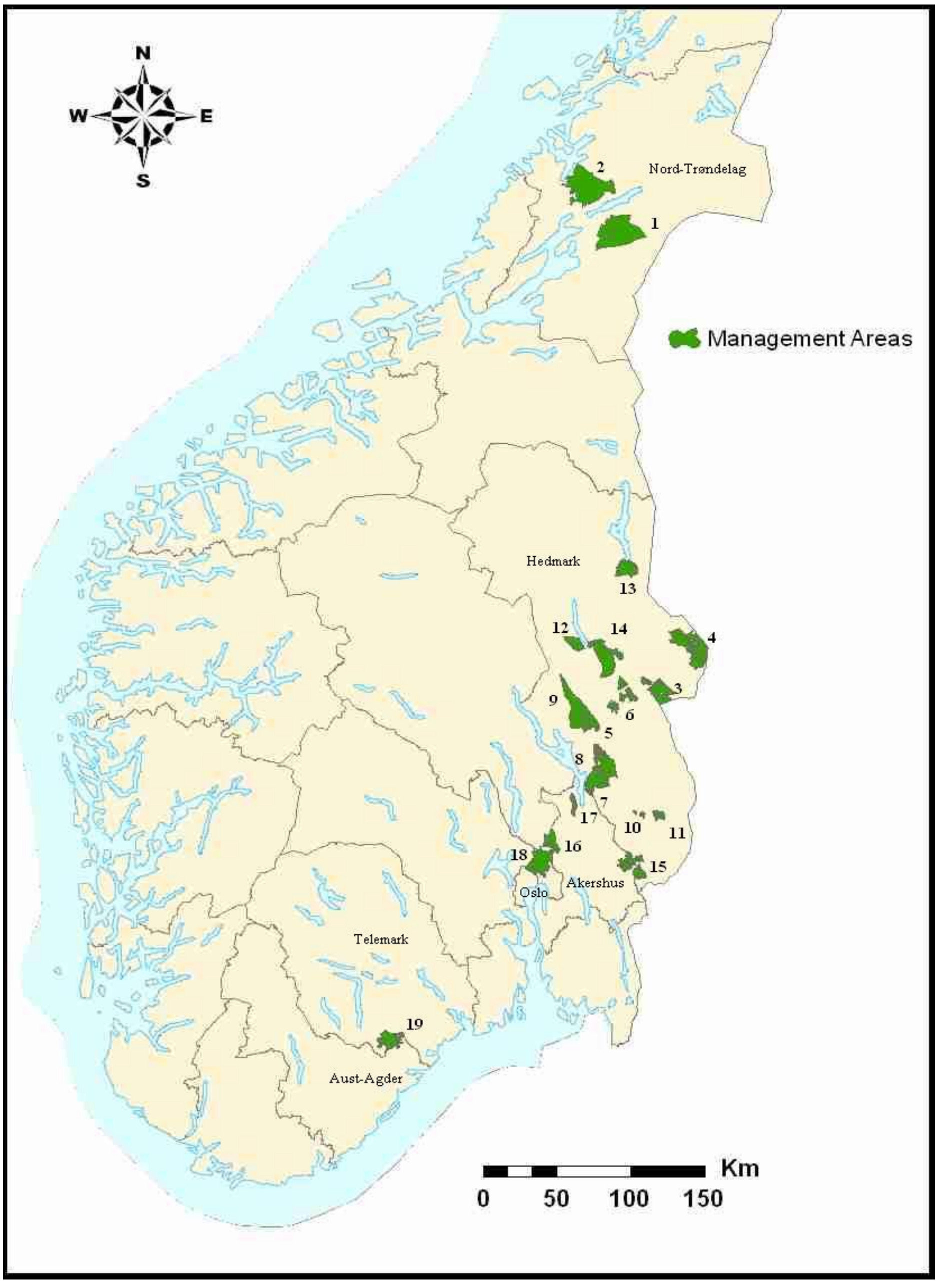

Figure 2. The management areas of forest grouse used in this study.

The two northernmost management areas are found in the county of Nord-Trøndelag; only one is located in the southern counties of Aust-Agder and Telemark, and the remaining 16 areas are found in the southeastern part of Norway in Hedmark, Akershus and Oslo counties.

The 19 areas included in this study are considered as separate management areas, each handling small game hunting on behalf of differently composed groups of public and private landowners. These categories of landowners range from one single private estate holder, to community-owned common land, to a mixture of private and public landowners, to Crown land, i.e., government-owned public land. The size of these areas ranges from 12 km^2 (a small, private landowner association in Hedmark) to 513 km^2 (a large area in Nord-Trøndelag with both private and public owners). An overview of these management areas, with estate type and size, is found in Appendix A-1.

It is not appropriate to give detailed landscape characteristics for each area, but a brief description at the regional level is useful. Large continuous forest areas dominated by spruce and pine are typical of the areas in the continental forests of Trøndelag, the eastern part of Hedmark and the south of Akershus. These areas are generally hilly, especial in Trøndelag with deep valleys form steep hillsides near the mountains. These areas have been highly impacted of forestry. The southern areas of Hedmark, as well as some areas further north, consist of a landscape with varying topography and continuous low alpine forest. Mountain birch dominates these areas, with low-productivity conifer forest in between, causing less intense forestry in these areas. Some areas in Hedmark are located within the lower alpine heathland region, which is characterized by a tundra-like, hilly area up to 1100 m above sea level. More alpine characteristics of the vegetation, including dwarf birch, heathland and meadows, are found here (Lande, 2011a). The southernmost area, in Aust-Agder/Telemark consists mainly of heathland and a varied but sparse forest, which is dominated by pine. The area is found mainly in the southern boreal and middle boreal vegetation zone, and is protected as forest reserve (Framstad, 2010).

2.2 Grouse Population Surveys - Density Data

In Norway, population surveys of grouse, which are performed as line transect censuses according to the distance sampling method (Buckland and Anderson, 2001), have been performed over the last decade through large-scale monitoring programs (Solvang et al., 2009). In Norway, distance sampling was systematically introduced in the late 1990s by a research project on willow ptarmigan. Later, it became the method on which Norwegian Institute for Nature Research (NINA) recommended the August censuses to be standardized (Brainerd et al., 2005) for all tetraonid species.

Within each management area, transect lines are distributed throughout the area, reflecting the landscape in the most representative way possible. An example is shown in Figure 3, which depicts the transect lines in two of the areas. The sampling is performed in August each year by hundreds of volunteers using trained pointing dogs. This system benefits both the management and the hunters, who get valuable training and information on bird densities before hunting starts in mid-September. The same transect lines have been used every year as far as has been practicable.

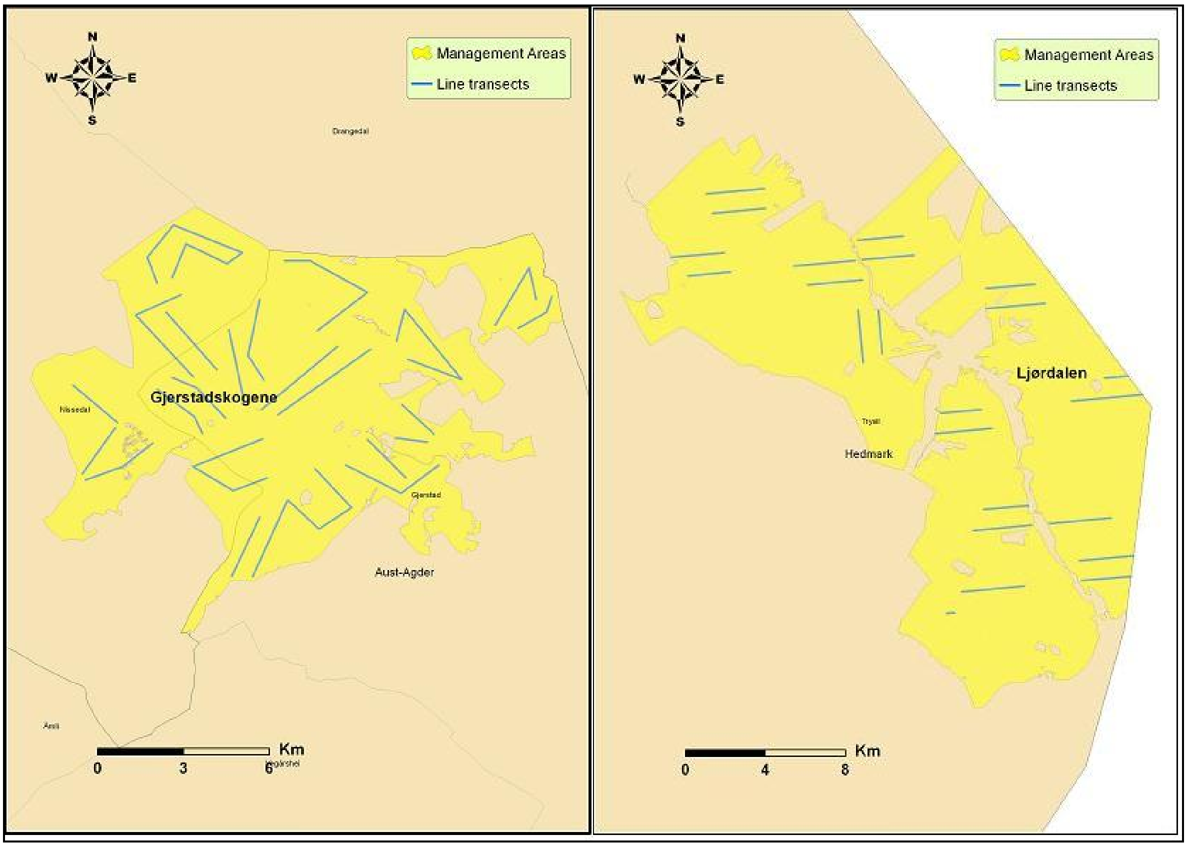

Figure 3. Line transects used during the august censuses of forest grouse performed in Gjerstadskogene and Ljørdalen, respectively.

The method is described in Moa et al. (2009), and is not described in detail in this study. Since 2006, these population surveys have continued under the auspices of the grouse management project. A relatively large amount of data on grouse species has been collected in these surveys. There is not as much data on forest grouse as on ptarmigans, but the amount of data increases, and the data quality improves yearly.

The results of these surveys (Appendix A-2) of black grouse and capercaillie densities form the basis of this thesis and consist of data collected from the period 2004 to 2010 in 19 management areas. Not all areas have been sampled every year, and for a few areas, results are available from only one or two years. Time series for 3 continuous years or more are available, however, for the majority of sites. It should be noted that, in this study, the overall density for each species has been used, rather than the adult density or the chick production, which data were also collected by the same censuses. The total density yields more robust data for the statistical analysis, with more variation and a larger sample size than would be obtained from split adult and chick numbers. Such an analysis has already been performed (with some of the same data) by Lande (2011a) as part of the grouse management project.

2.3 Geographical Information System (GIS) for Extraction of Data

ArcGIS Desktop version 10.0 from ESRI was used to produce various thematic maps and to extract data on landscape characteristics from digitised forest and vegetation maps as well as from national digital maps (FKB and AR50). Description of the datasets and extraction of variables from these is elaborated on in chapters 2.4.2 - 2.4.3.

To retrieve basis data for production of basic maps, WMS-services provided at the internet by the Norwegian Mapping Authority (GeoNorge, 2011) have been accessed directly from the ArcGIS tool.

Digitizing the Management Areas

To map the management areas into a spatial representation these needed to be digitised. The process to do this involved as the first step, collection of coordinates of the transect lines used and was available through the grouse management project or from representatives of the management area in question. Secondly, digitalisation of these lines if not already done, and lastly the management areas were digitised based on an overlay analysis of the transect lines and the national digital estate map (DEK from Norwegian Mapping Authority). Estates with a major part of a transect line contained within it was included in the respective management area. When the polygon forming the area was detected, the size of the management area was easily calculated by the GIS-tool. The polygons representing the management areas play a major role in all extraction of data from the various datasets, as well as the size do for calculations of the input variables used later on in the population analysis.

2.4 Data Collection

2.4.1 Identification and Selection of Plausible Explanatory Variables

Initially, there are many variables that could be appropriate as input for analysis to find possible influence to forest grouse density. The variables identified as potential explanatory variables of the population density analysis are listed in Appendix B-1. The data collection procedure implied search for information already available within the grouse management project and from different stakeholders and actors within grouse management. The stakeholders were identified as representatives of the 19 management areas and the county governor at the management side, research institutions NINA, UiO – University of Oslo, HiHM and HiNT, hunting associations locally and centrally (NJFF – The Norwegian Association of Hunters and Anglers) as well as other interest groups (NOF – The Norwegian Ornithological Society).

Quite a large part of the thesis focused upon collection and examination of these identified variables to decide which ones to ultimately use in the density analysis. This was done to ensure that the quality and quantity of the variables collected were good enough for statistical testing. The collected data was evaluated for criteria like relevance, applicability and reliability as well as sample size. Several of the potential input variables (Appendix B-1) to be used in the analysis had to be discarded due to failure to meet the evaluation criteria. Because there were too few samples available, this was the case for the density index of small rodents and birds of prey (the golden eagle and the goshawk). The harvest rate had to be discarded for the same reason. Small variations in the collected data were another reason to discard variables. Several of the management-related variables identified were excluded for this reason, e.g., all the hunting regulation variables (license regime, bag limit and period limitations) as well as protection of species by refuges and preservation of female birds from hunting. However, it should be noted that the data collected for the discarded variables have been structured and delivered to the grouse management project for storage, and these data are available for use in future analysis.

After the collection and evaluation period, the following 17 variables of four different categories were chosen as input to the population density analysis;

- *Habitat quality variables*: mean size of forest stands, proportion medium or high productivity class, proportion old forest, dominant wood type, SiD - landscape heterogeneity, proportion blueberry forest, proportion bogs, proportion forest cover.
- *Interference variables*: density of buildings, density of power lines and proportion of remote areas (i.e., areas > 0.3, 1 and 3 km distance away from roads and buildings).
- *Predator variables*: red fox density index, marten density index.
- *Management variables*: size of management area, type of management area.

2.4.2 Habitat Quality Data

The dataset of a forest map was downloaded from the website of The Norwegian Forest and Landscape Institute (SAT-SKOG, 2011). The SAT-SKOG map is based on satellite data from Landsat images (Gjertsen, 2007) and provides details of the forest resources, like type of forest, age and volume of forest stands among others. The dataset is based on images from 2007.

To calculate the following variables per management area, data were extracted from the SAT-SKOG dataset and used as described below.

- *Mean size of forest stands*: The size of each stand extracted and summarised and then divided by the number of stands within each management area.
- *Proportion of medium or high productivity class*: Productivity class and area of each stand were extracted, and the area of stands classified as medium or high productivity were summarised and then divided by the respective management area size.
- *Proportion of old forest*: Age and size of each forest stand extracted, and the area of each stand with an average age more than 80 years were summarised and divided by the respective management area size.
- *Dominant wood type*: Area and dominant wood type of each stand were extracted, and the total area of each dominant wood type was then summarised per management area. The wood type with the largest total area was appointed as the dominant.

Another dataset of a vegetation map was obtained from The Norwegian Directorate for Nature Management (SatVeg, 2010) via I. Herfindal (personal comm., 8.11.2010) at NTNU. This is also a digital map based on satellite data from Landsat images (Johansen, 2009). SatVeg attempts to reproduce the Norwegian nature and vegetation types and is divided into 25 vegetation classes and has an accuracy of 30 meters.

To calculate the following variables, data were extracted from the SatVeg dataset and used as described below.

- *Landscape heterogeneity – SiD* (Simpson's index of Diversity): Areas of vegetation classes containing (1) coniferous forest, (2) deciduous forest, (3) bogs and (4) "other" area types were extracted from the dataset, reclassified accordingly and finally the size of the reclassified areas were summarised. To measure the landscape heterogeneity, Simpson's index of Diversity (SiD) was used. The SiD was calculated by: $\mathbf{SiD = 1 - \sum p_i^2}$, where p_i = proportion of each vegetation class redefined, $i = 1 \rightarrow N$ where N = number of classes (4 in this case). The SiD ranges between 0 and 1, and the greater the value, the greater is the area's diversity. SiD is defined according to Simpson (1949).

- *Proportion of blueberry forest*: The size of blueberry forest areas was extracted and summarised, and it was then divided by the management area size.
- *Proportion of bogs*: The size of bog areas was extracted and summarised, and it was further divided by the management area size.
- *Proportion of forest cover*: The size of all areas containing forest of any type was extracted and summarised, and it was further divided by the management area size.

2.4.3 Interference Data

FKB and N50 datasets, downloaded from Norway Digital (2011), were provided by the Norwegian Mapping Authority. The FKB dataset was used for extraction of data on buildings and power lines, whereas the N50 dataset provided data on roads. The datasets were downloaded separately for each municipality.

The three variables measuring the proportion of an area more than specified distance from buildings and roads (0.3 km, 1 km and 3 km, respectively) was obtained stepwise: 1) All the layers containing buildings for all municipalities involved were merged; 2) An overlay analysis with the management areas was performed to cut off buildings outside the management areas. A buffer zone around the management areas was used to retain buildings at the specified distance; 3) The management areas were then cut in a new overlay analysis with the resulting layer from step 2; 4) Step 1 – 3 were repeated for the roads; 5) The remaining areas from the two cut operations above were then intersected in a final overlay analysis, and the size of the resulting polygon was calculated. An example of the management area Ljørdalen is shown in Figure 4.

Note! An inspection of the extracted variables showed very little variation in the variable measuring areas more than 3 km from roads and buildings. Only 3 of the 19 management areas appeared to have such remote areas at all. For this reason, this variable was excluded from the statistical analysis. Additionally, a correlation test of the variables measuring remote areas at a distance more than 0.3 km and 1 km away showed a significant, high correlation ($r = 0.94$, $N = 18$, $p < 0.001$). Hence, keeping both variables would add very little to the analysis; the 0.3 km variable was consequently discarded.

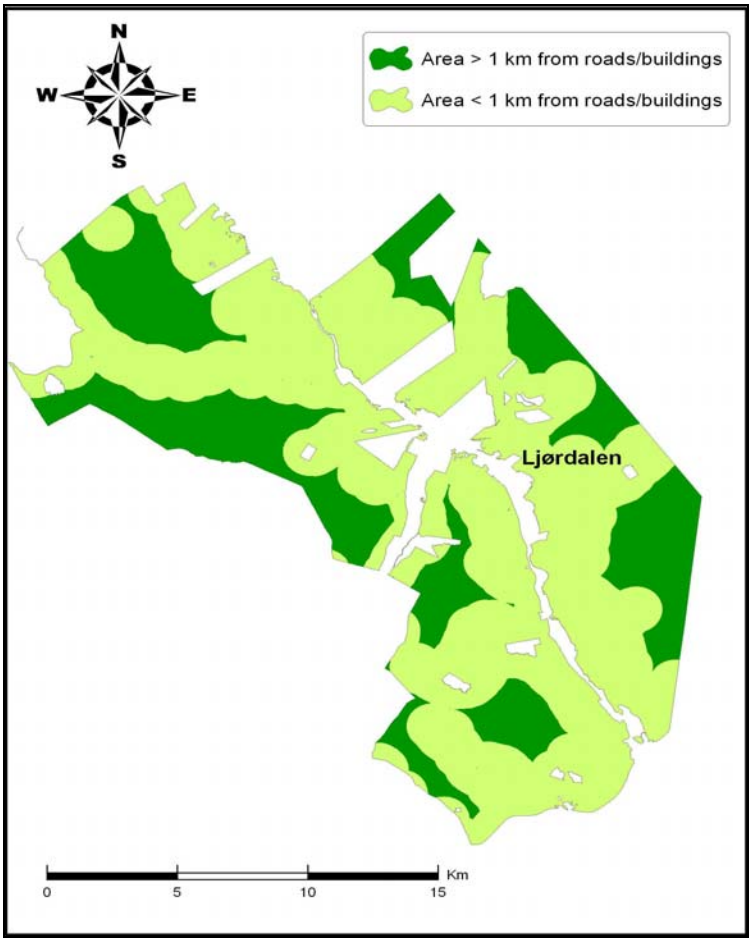

Figure 4. Areas in Ljørdalen management area more than 1 km away from roads and buildings in dark green colour.

The density of buildings in the management area was obtained stepwise: 1) All the layers containing buildings for all municipalities involved were merged; 2) An overlay analysis with the management areas was performed to cut off buildings outside the management areas (no buffer zone used); 3) The buildings remaining within the management area were counted and subsequently divided by the area size.

Power line density within the management area was obtained stepwise: 1) All of the layers containing power lines for all municipalities were merged; 2) An overlay analysis with the management areas was performed to cut off power lines outside the management areas; 3) The lengths of the power lines remaining within the management area were summarised and subsequently divided by the area size.

2.4.4 Predator Data

Data on the red fox and pine marten populations were collected from line transect censuses originally intended for sampling lynx (*Lynx lynx*) populations at winter. These surveys are preferably performed each year between January and February by volunteers under the regionally direction of NJFF. The surveys are described by Brainerd et al. (2005) and are performed at the community rather than the local level, within the management areas; however, the censuses are assumed to be representative to the densities of foxes and martens in their respective management areas. In short, the line transects used are approximately 3 km in length with a density of 3 lines per 100 km^2 and are distributed within the terrain such that they are supposed to capture the movements of lynx in the area. The number of fresh fox and marten, as well as lynx, footprints intersecting the line-transects in a 24-hour period are recorded, preferably immediately after snowfall.

Not all management areas have been covered by these surveys, but time series from the 2003-04 season through the 2009-10 season for all areas in the counties of Hedmark (except one area) and Nord-Trøndelag are available; these were collected from HiHm and NJFF and include 14 areas in total.

2.4.5 Management Data

The only remaining management and hunting variables identified initially (Appendix B-1) after the quality evaluation was performed, were the type and the size of the management areas. These two variables are already explained in chapter 2.1 and 2.3, respectively.

The harvest rate was discarded as an explanatory variable to the forest grouse density the subsequent year due to lack of data. In most of the areas, the data obtained were partly unreliable, and the low reporting level among the hunters yielded too few reported results. Hence, it was impossible to get sufficient data on harvest rate to use this parameter in statistical analysis.

2.5 Statistical Analysis

All statistical analysis was performed using the free software R version 2.10.1 (R Development Core Team, 2010). Separate statistical analysis of population density estimates of the two species was performed. Because density estimates were available for multiple years in most of the areas, and because observations in different areas the same year might be correlated if the temporal dynamics are correlated across space (Kvasnes et al., 2010), the observations could not be considered as independent data points. To account for this pseudoreplication (Hurlbert, 1984), linear mixed effect models (LME) with year and management area as random factors were applied in all model analyses. To stabilise residuals and to avoid predicting negative densities, the density estimates of black grouse and capercaillie were log-transformed prior to analysis.

Model selection

The population density estimates were analysed using separate global models for each of the different input variable categories; i.e., separate model selection procedures were performed for the habitat quality variables, the interference variables, the predator variables, and the management variables. The variables from the best-ranked model in each category were then used in a final selection procedure to find the best overall model for each species.

During model selection procedures, the models were fitted by use of maximum likelihood, and the Akaike's Information Criterion corrected for small sample size (AICc), was used to determine the best-ranked model (Burnham and Anderson, 2002). If several models were within a ΔAICc < 2 compared to the best-ranked model, then the principle of parsimony was applied, i.e., the simplest model representing the response adequately was selected (Box and Jenkins, 1970).

To cope with the high number of explanatory variables in the search for the best model, an important restriction on the modelling procedure was introduced by allowing only 4 main effects and one two-way interaction in the same model. With this restriction, all possible variable combinations within each category were tested, starting with the simplest models (with the main effects only), through the most complex models allowed (4 main effects and one two-way interaction).

To avoid colinearity in the models (i.e., two or more explanatory variables in the same model correlate internally), principal component analysis (PCA) was run prior to the global model determinations. The habitat quality variables; size of forest stands, productivity, bogs, and forest cover were found to be highly correlated (Appendix C-1), and were consequently combined into one variable by a PCA-procedure. Among the variables involved in the final selection procedure, the variables; proportion of remote areas, area size and forest cover correlated significantly (Appendix C-2), and were combined into one variable by a new PCA-procedure. If the PCA-score was found to be in a model among the best-ranked models (i.e., within a ΔAICc < 2), each of the PCA-components were tested in separate models, in case these were ranked higher than the already-identified best model.

All of the PCA-procedures contributed simultaneously as side effects to reducing the number of explanatory variables in the global models. The habitat quality variables were reduced in number from 8 to 5 this way, and for the final analysis the number of variables was reduced to 6 and 5 for black grouse and capercaillie, respectively. The global models are explained in detail for each variable category in chapter 3.

Number of observations

The density estimates of black grouse and capercaillie, as listed in Appendix A-2, was available for a total of 89 samples for black grouse and 85 for capercaillie in the 19 areas. When analyses were performed involving variables of the habitat quality category or the management category only, samples of all explanatory variables in every area were available. The sample size was reduced when the other two parameter categories were involved as a result of lack of data in some of the management areas. Table 1 summarises the sample size within each type of variable category.

Table 1. Number of complete observations when different variable categories were involved in the model analysis.

Variable category	Sample size black grouse	Sample size capercaillie
Habitat quality variables	89	85
Management variables	89	85
Interference variables	84	80
Predator variables	66	67
Final analysis with variables from all categories	66	67

For the interference category, no data on power lines and buildings were available in Oslomarka. Additionally, no data on predator densities were available in 5 areas because no line transects sampling for predators in winter have been performed in these areas. These areas were the following: Gjerstadskogene, Oslomarka, Råsjø, Minneåsen, and Stangeskovene (Appendix A-1).

3 Results

An initial analysis of the density estimates showed an average density in each of the 19 areas ranging from 2.4 to 12.9 of black grouse per km^2, with a grand mean of 4.3 ± 2.4 SD (Figure 5). The maximum density of black grouse measured within a single area was 19 birds per km^2, while the minimum was 1.3. For capercaillie, the density ranged from 1.4 to 9.3 birds per km^2, with a grand mean of 3.5 ± 2.5 SD. The maximum density of capercaillie was 16 birds per km^2, while the minimum was 0.2. In general, the densities of the two species were significantly correlated ($r = 0.37$, $N = 84$, $p < 0.001$).

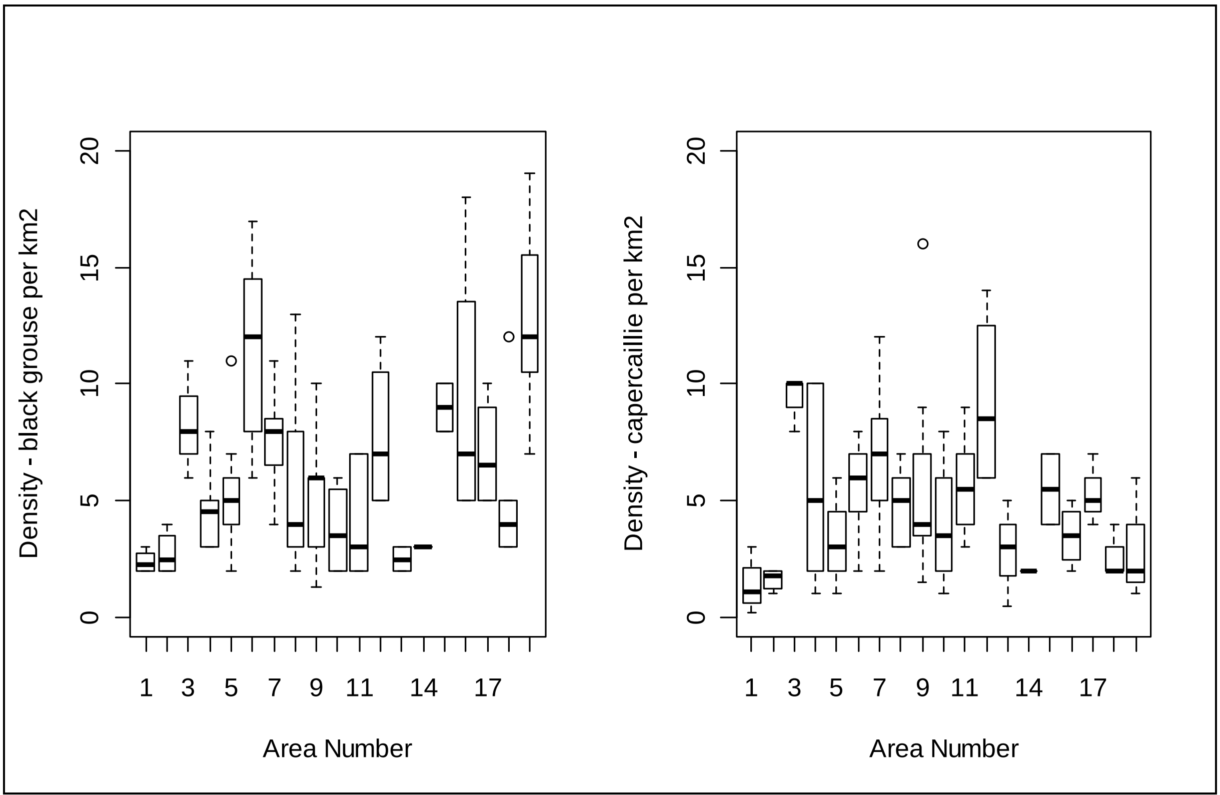

Figure 5. Box plots of the temporal variances in density within management areas are shown in the figures. The black grouse populations are shown to the left and capercaillie populations are shown to the right. The name of each management area corresponds to an area number in Appendix A-1. Each box shows the median value and its 1st and 3rd quartile in addition to the maximum and minimum values.

As will be shown in the selection procedure for habitat quality variables in chapter 3.1, the forest cover variable was not contained in the selected model for black grouse, and separate PCA-procedures were consequently needed for the two species. The resulting global models of all the variable categories are listed in Table 2.

Table 2. Global models for all variable categories. See Appendix B-2 for description of variable acronyms used in the models.

Variable category	Species	Variables of the global model
Habitat quality variables	Both	OldF, WType, SiD, Bogs, and the PCA-score. PCA-score: Stands, Prod, BForest, and ForestC.
Interference variables	Both	A1km, DensP, and DensB.
Predator variables	Both	Fox and Marten
Management variables	Both	AreaSize and AreaType
Final analysis with variables from all categories	Black grouse	WType, SiD, Marten, Fox, DensP, and PCA-score. PCA-score: AreaSize and A1km
	Capercaillie	BForest, Marten, Fox, AreaType, and PCA-score. PCA-score: AreaSize, A1km, and ForestC.

3.1 Model Selections

The results from the model selections are presented separately for each variable category in Table 3. Details of each model presented can be further studied in Appendix C-3, which includes the estimated fixed effects and the corresponding standard errors. Acronyms of the variables used in the models are listed in Appendix B-2.

In the following paragraph, the results of the model selection procedures for the habitat quality variables are explained. The remaining selection procedures are similar and have not been elaborated in detailed. See Table 4 for clarification of the results.

According to Table 3, only two models for the black grouse were within the selection criteria of $\Delta AICc < 2$. Model 1 is the simplest model and was selected as the best reflection of the variation in the estimated population densities. This model consists of two fixed factors: the dominant wood type (WType) and the landscape heterogeneity (SiD). In addition to the main effects from both of these, an interaction component affects the predicted population density. For capercaillie, four models are within the selection criteria of $\Delta AICc < 2$ (Table 3). Again, Model 1 is the simplest model and was selected as the best-fitted model. Additionally, this model consists of two fixed factors: the proportion of forest cover (ForestC) and the proportion of blueberry forest (BForest). In addition to the main effects from both of these, there is an interaction component affecting the predicted population density.

Table 3. Model selection table for all variable categories. Models are ranked according to ΔAICc-values. The selected model within each variable category is presented in bold.

Step 1 - Habitat quality analysis:			**AICc**	**ΔAICc**
Species	**Rank**	**Fixed factors of LME-model**		
Black grouse	**1**	**WType * SiD**	**148.60**	**-**
	2	WType * OldF + SiD	150.10	1.50
	3	WType * SiD + PCA-score	150.69	2.09
Capercaillie	**1**	**BForest * ForestC**	**182.48**	**-**
	2	BForest * ForestC + WType	182.60	0.12
	3	BForest * ForestC + OldF	182.77	0.29
	4	BForest * ForestC + SiD	184.12	1.64
	5	BForest * PCA-score	187.86	5.38
Step 2 – Interference analysis:				
Black grouse	**1**	**A1km * DensP**	**141.96**	**-**
	2	A1km * DensP + DensB	143.74	1.78
	3	A1km	145.75	3.79
Capercaillie	1	A1km + DensP	171.76	-
	2	**A1km**	**172.21**	**0.46**
	3	A1km + DensP + DensB	173.17	1.41
	4	A1km + DensP * DensB	173.69	1.93
	5	A1km * DensP	173.72	1.96
	6	A1km + DensB	173.80	2.04
Step 3 – Predator analysis:				
Black grouse	**1**	**1 (i.e., intercept only)**	**119.87**	**-**
	2	Marten	121.49	1.62
	3	Fox	121.81	1.94
	4	Fox + Marten	123.62	3.75
Capercaillie	**1**	**Marten**	**153.52**	**-**
	2	Fox + Marten	155.47	1.95
	3	1 (i.e., intercept only)	157.11	3.59
Step 4 – Management analysis:				
Black grouse	**1**	**AreaSize**	**152.28**	**-**
	2	AreaSize * AreaType	154.50	2.22
Capercaillie	**1**	**AreaSize + AreaType**	**178.51**	**-**
	2	AreaSize * AreaType	180.22	1.71
	3	AreaType	182.74	4.23
Step 5 – All categories analysis:				
Black grouse	1	WType * SiD + AreaSize	116.46	-
	2	**A1km**	**117.14**	**0.69**
	3	WType * SiD	117.25	0.79
	4	PCA-score	117.56	1.11
	5	WType * SiD + PCA-score	117.70	1.24
	6	WType * PCA-score + SiD	117.70	1.24
	7	SiD * PCA-score + DensP	117.88	1.42
	8	WType * DensP + SiD	118.46	2.00
Capercaillie	**1**	**PCA-score * BForest + Marten**	**130.12**	**-**
	2	PCA-score * BForest + Marten + Fox	130.91	0.78
	3	PCA-score * BForest + Marten + WType	132.34	2.21

For matter of clarification, the best-fitted models for all categories are summarized in Table 4.

Table 4. Overview of the model selected as the best-fitted model within each variable category. All models are LME-models with year and management area as random factors.

Variable category	Species	Fixed factors of best LME-model
Habitat quality variables	Black grouse	WType * SiD
	Capercaillie	BForest * ForestC
Interference variables	Black grouse	A1km * DensP
	Capercaillie	A1km
Predator variables	Black grouse	1 (i.e., intercept only)
	Capercaillie	Marten
Management variables	Black grouse	AreaSize
	Capercaillie	AreaSize + AreaType
Final analysis with variables from all categories	Black grouse	A1km
	Capercaillie	PCA-score * BForest + Marten

It is worth considering the result of the selection process for the predator category for the black grouse because neither the fox nor the marten density index showed any influence on the bird density, i.e., the intercept was ranked higher (Table 3); however, biological evaluation calls for these factors to be analysed more thoroughly because it is known that predators play an important role on bird populations in general. One possibility is an interaction effect with some of the variables in the other categories that would make fox and marten significant influences on the density of forest grouse populations. I consequently included these two variables in the overall analysis with variables from all categories.

For the black grouse, it is noteworthy that the model selected during the analysis of the habitat quality category, Model 1 in Table 3, is still ranked among the best models in the final analysis.

3.2 *Model Predictions*

The predicted fixed effects of the selected models for the habitat quality category and for the final analysis are visualized in Figure 6. The effects of the best-fitted models obtained during the interference, predator and management selection processes are not shown hereafter because these are only intermediate results with limited interest for the final analysis.

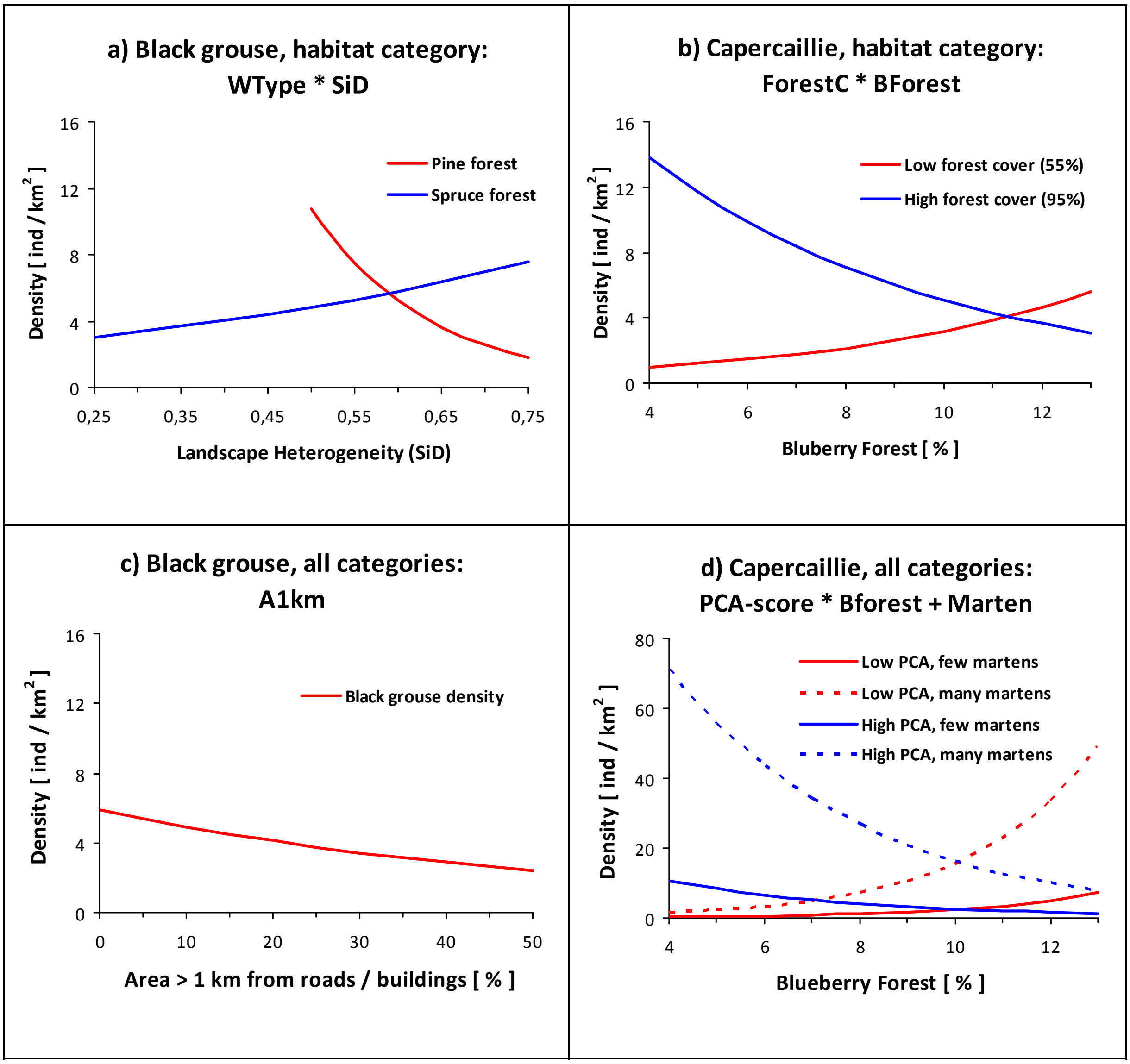

Figure 6. Fixed effects of the best-fitted models visualized. Models analysed by habitat quality variables at the top (a, b), and by variables from all categories at the bottom (c, d). Black grouse models are at the left and capercaillie models are to the right.

Starting with predicted effects of the habitat quality variables on black grouse (Figure 6 a), it is worth considering the diametrically opposed effects in pine- and spruce-dominated forests. Although in spruce-dominated forests, the density increases slightly with increasing landscape heterogeneity, the contrary effect is observed in pine forests. In spruce forest, an increase in the landscape heterogeneity from 0.5 to 0.6 leads to an increase in the population density from 4.8 to 6.8 black grouse per km^2 (+ 20%), whereas a similar change in pine forests will lower the density from 10.7 to 5.2 black grouse per km^2 (- 51%). The limited range of the graph in pine forest is also noteworthy (Figure 6 a).

For the capercaillie (Figure 6 b), when the forest cover is low, the population density is slightly increased as the proportion of blueberry forest is raised. For high forest cover, the density is lowered when blueberry forest is increased. If forest cover is low (55%), an increase in blueberry forest from 10% to 11% leads to a raise of the density from 3.1 to 3.8 capercaillie per km^2 (+ 21%), whereas a similar change in blueberry forest when the forest cover is high (95%) will lower the density from 5.1 to 4.3 capercaillie per km^2 (- 15%).

When the full model with variables from all categories in the analysis is used, then the density of black grouse is lowered when the remote areas increase (Figure 6 c). An increase in the remote areas from 20 to 30% leads to a decrease in the population density from 4.1 to 3.4 black grouse per km^2 (- 16%).

The full model selected for analysis of the capercaillie density (Figure 6 d) is quite complex to interpret, but it shows that if many martens are present in an area, then the capercaillie density is high too, and that an increase in blueberry forest is positive to the capercaillie density if the PCA-score is low but is negative if the PCA-score is high. Starting with a low PCA-score (- 3.76), then a change in proportion of blueberry forest from 10 to 11% with few martens present (index = 0.05) will increase the density from 2.4 to 3.5 capercaillie per km^2 (+ 47%). A similar change with many martens present (index = 1.20) will increase the density from 15.5 to 22.7 capercaillie per km^2 (+ 47%). With a high PCA-score (1.95), a change in blueberry forest from 10 to 11% with few martens present will decrease the density from 2.5 to 2.0 capercaillie per km^2 (- 22%), whereas a similar change with many martens present will decrease the density from 16.4 to 12.9 capercaillie per km^2 (- 22%).

The random factors used in all LME-models, i.e., the variables; management area and year, explain a certain part of the density variance of the populations. In the model selected as the best-fitted model reflecting the black grouse density, the factor year accounted for 16% of the density variance while 34% was due to management area. For the best model reflecting the capercaillie density, these numbers were 28% and 0% for year and area, respectively. The unexplained remainder of the variance is accounted for by the sampling procedure and results from different sources of error during the population censuses.

4 Discussion

For black grouse, in the model selection procedure with the habitat quality variables (Table 3), all of the highest-ranked models include dominant wood type and landscape heterogeneity, justifying the selection of the simplest model that contains both these factors. In the final selection procedure, the same model was ranked third and is considered as the second-best model after applying principle of parsimony. Additionally, several of the other highest-ranked models include both these habitat factors. These results support the identification of wood type and landscape heterogeneity as important for the black grouse density.

A high diversity index indicates a landscape of high mixture of coniferous and deciduous forest in a various topography admixed with humid bog areas and open moorland. Such a landscape seems to create good black grouse habitats because it provides shelter, escape routes and enough food to the birds. A diverse landscape forms edges as a result of transitions between landscape types and a changing topography. Edges and open areas provide the birds with escape routes from predators and hunters, but may also serve as shelter from e.g., birds of pray in junctions towards denser vegetation (Wegge and Kastdalen, 2007). Humid areas, provided by bogs, are especially important to the chicks because they eat insects and larvae in the first weeks after hatching (Wegge and Kastdalen, 2008, Baines et al., 1996). In general, a landscape with small patches of different area types provides a diverse diet to both adult birds and their chicks. The importance of a high landscape diversity for black grouse has been described by several authors, e.g., Lande (2011a) in a recent study, Hjeljord (2008), Kurki (2000) and Swenson and Angelstam (1993).

The parameter effect of the model selected during analysis of the habitat variables (Figure 6 a) shows that black grouse density in pine forest is limited by landscape heterogeneity (ranges only from 0.5 to 0.75). This observation is likely a result of the low number of observations in pine-dominated forests; i.e., black grouse were observed in only 3 such areas, for a total of 15 observations. In the spruce-dominated areas, the landscape heterogeneity ranged from 0.25 to 0.75 and was based in 16 areas with a total of 74 observations. For this reason, the results should not be generalised to other black grouse habitats. If we extrapolate from the graph and let the landscape heterogeneity vary throughout the same range as observed in spruce-dominated forest, then the black grouse population is predicted to reach a density of 65 birds per km^2, which is not a realistic density for the species, especially not in a low-diversity landscape. As a result of the low number of observations from pine forest, and because a biological explanation would support an increase in population density with increasing landscape diversity, this model should be considered as supporting the importance of landscape heterogeneity to black grouse populations. This interpretation is also supported by Lande (2011a) in her recent study. In that study, landscape diversity was defined via the SAT-SKOG dataset; I have used the SatVeg dataset for this purpose. The results of the studies are similar for the black grouse, but not for the capercaillie. Lande (2011a) proved that landscape diversity is an important determinant of density for both species; however, the trend of decreasing black grouse density in pine forest observed in this study is still worthy of consideration.

For capercaillie, in the model selection procedure with the habitat quality variables (Table 3), all of the 4 highest-ranked models include forest cover and proportion of blueberry forest. Additionally, in the final selection procedure, all of the models ranked highest include both these factors, since the forest cover is represented by the PCA-score; thus, the confidence is high in identifying forest cover and proportion of blueberry forest as important habitat factors to the capercaillie density. If the predicted effects of the best models in the two selection procedures are compared, (Figure 6 b and d), a similar pattern in the red and blue graphs can be observed as the blueberry forest cover increases. This occurs because the forest cover is included in both models. Analysis of the PCA-components shows that the forest cover is the most varying component, accounting for as much as 85% of the total variance in the PCA-score. The other two components (the management area size and the proportion of remote areas), account for 5 and 10%, respectively. An inspection of the dataset shows that a strongly negative PCA-score represents a low forest cover in an area, whereas a strongly positive PCA-score indicates a high proportion of forest cover. The observation of the similar pattern strengthens the acceptance of forest cover and blueberry forest being important factors in a good capercaillie habitat in August.

Because the capercaillie is associated with the large, continuous boreal forest, the importance of a high forest cover indicated in this study supports previous findings by Seiskari (1962), and Swenson and Angelstam (1993). The large boreal, conifer forests provides shelter to the capercaillie which is important with respect to predation from e.g. the goshawk (Selås et al., 2008, Wegge and Kastdalen, 2007). The importance of blueberry forest to capercaillie chicks has been demonstrated previously by Wegge and Kastdalen (2008), but are in general important to forest birds (Selås, 2000, Hjeljord, 2008).

A high forest cover does; however, not always lead to a positive response of capercaillie density because the graph is decreasing with increasing blueberry forest. In Figure 6 b and Figure 6 d, the cross-over occurs at a proportion of approximately 10-11% blueberry forest, suggesting that a low forest cover is better when the content of blueberry forest is high in an area. Baines et al. (2004) suggest, in a study from Scotland, that the breeding success of capercaillie increases with increasing blueberry forest cover, but does not continue to improve above a cover of 15–20%. In areas with a low forest cover, the red graphs of Figure 6 b and Figure 6 d are supported by Baines et al. (2004) at low levels of blueberry forest, but the graphs do not show any trend of flattening above a cover of 12 – 13%, which is the maximum blueberry forest cover in my study areas. The proportions of blueberry cover may not be comparable in these studies, in part because the samples are derived from different sites, but also as a result of the extraction methods used for detection of blueberry forest cover. I.e. vegetation classification on the digitalised maps used may differ, as may the GIS method used for data extraction. Wegge and Kastdalen (2008) also demonstrated the importance of blueberry forest to the capercaillie broods, but in areas of high forest cover, the decline in capercaillie density with increasing blueberry forest cover is seldom reported. This study, however, suggests that both the proportion of blueberry forest and total forest cover are important, but it is unclear how the parameter effects relate to each other.

In the final model selection procedure for black grouse, the best model identified the proportion of remote areas as a factor affecting the black grouse density; however, the effect is negative (Figure 6 c), decreasing the density with an increasing proportion of such areas. In the interference analysis of capercaillie (Table 3), the best model also contained only the proportion of remote areas, and the effect appeared to be negative (Appendix C-3) in this case as well. This result confirms the selected model for black grouse. These results are difficult to explain biologically. It is possible that roads and building constructions create open areas, to which the black grouse previously has been proven to adapt to well (Swenson and Angelstam, 1993). The previously studied areas, however, emerged from forestry, not secondarily from the construction of infrastructure. It is more likely an underlying factor not identified by this study causes spurious effects in the analysis (e.g., the proportion of remote areas may be a confounder to this unidentified factor). An alternative explanation may be that the inclusion of some of the large management areas of this study with large remote areas lowers the average density just by chance. This hypothesis may explain the case for the two large areas in

Trøndelag, in which the density estimates have been very low in recent years (Appendix A-2). See the section below discussing data quality for further discussion of this topic.

The effect of marten abundance, according to the model (Figure 6 d), is complex and intriguing. In an area with high forest cover (i.e., high PCA-score (blue lines)), and low content of blueberry forest (i.e., ≈ 4%) an increase in the marten density index from 0.05 to 1.20 is associated with a predicted capercaillie population increase from roughly 10 to 70 birds per km^2, which is an unlikely density. On the other hand, a similar change in marten index in areas of low forest cover but with a large proportion of blueberry forest (i.e., ≈ 13%) is associated with a predicted increase in the population of roughly 40 birds per km^2 as well. A significant, positive correlation was also found between pine marten and capercaillie ($r = 0.29$, $N = 67$, $p = 0.017$) strengthening a model selection containing marten as a fixed variable. The alternative prey hypothesis predicts that the populations of forest grouse and pine marten will fluctuate in synchrony with the small rodent cycle. Consequently, during small rodent lows, the marten utilises forest grouse to a greater extent. A top in the small rodent cycle may often reveal its existence in late winter or in spring if the breeding conditions beneath the snow cover have been optimal. The growth may continue throughout the summer and fall, causing low predation of forest grouse and good conditions for the chicks to grow up. If, however, during a presumptive small rodent top these populations collapse, e.g., from a disease outbreak, the consequences for the forest grouse populations may be disastrous if this collapse occurs in the spring or early summer. Such a collapse may force the predators to switch from the small rodents to grouse species as its main pray. In 2005, such a collapse occurred in Trøndelag and in areas further north; some grouse populations suffered until recently as a result. Brainerd and Rolstad (2002) demonstrated that the pine marten's habitat use is consistent with the habitat preferences of important prey; thus, a good capercaillie habitat should be a good marten habitat. Other studies, however, do not support these results; Baines et al. (2004), for example, could not demonstrate that the pine marten index is related to capercaillie breeding success in the UK, while Kurki et al. (1997) indicated that the relative densities of both red fox and pine marten in Finland negatively correlate with the proportion of grouse hens with a brood in August.

The small rodent index was suggested as an important focal variable at an early stage in this study, but unfortunately not enough relevant data are available to conduct a proper statistical analysis. Some data exist at HiNT, HiHM, UiO and at NINA, but only data collected by HiNT and NINA are useful for this study.

The red fox was expected to affect the density of forest grouse, as previously demonstrated by a number of studies (Angelstam et al., 1984, Rolstad, 1989, Kurki et al., 1998, Wegge and Kastdalen, 2007). Foxes are included in the second-best-ranked model in the final analysis for capercaillie, but the negative effect (Appendix C-3) is low, compared with the positive effect associated with marten population growth. For black grouse, both marten and red fox were included as factors in the final analysis, but neither of these showed up in any of the potential best models. Hence, from this analysis there is no reason to consider any of these predators as important to black grouse densities. This result is quite unexpected, because several other studies referred to above demonstrated both pine marten and red fox to be important factors to the density of black grouse. The reason may be low data quality of the density indexes estimated for the two predators during the winter censuses. Despite that red fox and pine marten do not prefer the same habitats (Kurki et al., 1998, Brainerd and Rolstad, 2002) and that the fox may displace the marten from an area, especially during small rodent lows, it is reasonable to expect the density indexes of the species to correlate to a certain extent. Because no significant correlation was found ($r = 0.08$, $N = 96$, $p > 0.05$) the quality of the predator density index is not strengthened. Another reason may be that the predator estimates may not represent the correct density 7 – 8 months later in August, when the forest grouse censuses are performed.

A high density of power lines is expected to affect the forest grouse densities negatively. This variable was included in the best models of both black grouse and capercaillie when only the interference variables were analysed (Table 3). In the final analysis, it was retained as a variable in two of the relevant best models for black grouse but was included in the lowest-ranked models. Power line density, however, negatively affects black grouse density (Appendix C-3) in this study and supports previous findings, e.g. by Bevanger (1995).

Data quality

When the model selected for black grouse was evaluated, the large management areas in Trøndelag with low density estimates in the recent years was pinpointed as a possible reason for the negative effect associated to an increase in the proportion of remote areas. When these areas are thoroughly inspected on the map, they are often revealed to be mountain areas with sparse vegetation. Hjeljord (2008) describes both the black grouse and the capercaillie to be inhabitants of the boreal coniferous forest, in which they utilise different succession stages of the forest (Seiskari, 1962, Swenson and Angelstam, 1993). Mountain areas are normally not considered as good habitats for the forest grouse, although grouse are found in these regions

(Bollmann et al., 2005, Storch, 1993). The inclusion of mountains may thus account for the decreased density of both species when the proportion of remote areas is increased. The management areas in Trøndelag, as well as a couple of areas in Hedmark, include large mountainous regions between the forested valleys and hillsides. It is possible that these areas should have been redefined because most of the variables used in the analysis are affected by total area size, which lowers their value in most cases. A similar argument may also be applied to large lakes in the management areas. Before the data were extracted from the digital maps, I decided to include both mountains and lakes, considering them as natural parts of the landscape forming a forest grouse habitat. Because this decision may have resulted in a systematic, methodical error, it will be worthwhile to thoroughly investigate potential corrections. An alternative way may be to incorporate these geographic features as separate variables in the statistical analysis and let the model selection procedure accept or reject them as important variables.

The quality of the grouse population density estimates (Appendix A-2) is an issue for discussion, and it may be questionable if some of the areas included should have been excluded. This evaluation is based mainly on the size of the areas (Appendix A-1), the annual total length of sampled transects and the resulting confidence interval within each sampled area. In some of the areas, the total sampled transect length is short despite being large areas. For comparison, the Romedal Almenning area has got a sampled transect length of approximately 30 km annually, while an area of similar size, such as Vang Almenning has got a length of 120 - 130 km. In 2007, Romedal had a density of black grouse of 8 (4 – 15) birds per km^2, while Vang in 2010 had a density of 10 (8 – 14) birds per km^2. The uncertainty is higher (the confidence interval is larger) when the sampled transect length is short. According to the distance sampling method (Buckland and Anderson, 2001) 40 observations are desirable to obtain a good density estimate, which is a challenge in years with a low density of forest grouse. Experience and level of trained personnel, quality of the pointing dogs used, weather conditions, landscape types and an area's topography are some of the vital factors decisive for the sampled transect length needed to obtain at least 40 observations. The two latter factors are not changing, but the personnel, dogs and the weather do as well as the forest grouse density. According to Solvang et al. (2009) the results of the censuses are especially sensitive in forest areas in weather conditions with high temperature and low humidity, and the grouse density may easily be underestimated. A similar effect is also expected if the weather conditions are extreme in other ways, i.e., very windy or heavy rainfall. In this study, I considered the sample size as very important for the statistical analysis, and consequently included as many areas and annual measurements as possible. An area was included only if the samples were considered to be reliable, either due to several consecutive annual censuses in the area, relatively small confidence intervals, or because the sampled transect length was long relative to the size of the area.

Suggestion of improvements

As described in chapter 2.4.5, the harvest rate had to be discarded as an explanatory variable to the grouse densities the subsequent year due to lack of data. Several management areas reported the number of hunting days used, and because the number of birds reported shot each year were known, an annual hunting index measuring the efficiency of the hunt in each area was calculated. This index is not useful as an explanatory variable, but could be used as support to the population density estimates in case of a positive correlation. For black grouse, no significant correlation between the hunting index and the estimated density was found ($r = 0.16$, $N = 41$, $p > 0.05$), but a significant, positive correlation was found for capercaillie ($r = 0.43$, $N = 37$, $p = 0.008$). Although there was a significant correlation for the capercaillie, which can be interpreted as a support to density estimates of that species, no such support was found for the black grouse. These results do not strengthen the quality of the density estimates, but do not weaken them either; however, because the harvest rate is not available in most of the management areas, I consider the hunting statistics currently collected to be of an insufficient quality for use in scientific analysis. Hence, the reporting system used should be improved and must be harmonized among the involved management areas. How to improve the reporting is yet an open question, but incentives to the hunters to perform the reporting must be identified.

The volunteer population censuses used today is time-consuming but extremely valuable for both management and research. For managers, the density estimates are important for regulating the harvest rate, both in time and in space. For researchers, it is desirable to obtain longer time series of the density estimates to increase the reliability of the dataset. If the sample size is increased, the probability of selecting observations that are independent with respect to both time and space will be improved. Random selection of observations from a large pool of samples will become possible if the population censuses within the current management areas continue in the future. An increased sample size may be obtained by adding more management areas to these annual censuses, but for continuity and longer time series, it is preferable to stick to the areas already included.

5 Conclusion

I suggest increased landscape heterogeneity to be considered as a positive factor to the black grouse density in management areas dominated by spruce. A high diversity in the landscape creates good black grouse habitats. In management areas dominated by pine, there was a weak indication of a negative impact on the density of black grouse from increased landscape heterogeneity; however, I reject to generalise this result as valid to all pine-dominated forests because the dataset consists of too few observations in this type of forest.

For the capercaillie, I suggest to consider both proportion of forest cover and proportion of blueberry forest in a management area as factors affecting the density. The capercaillie density will increase if the proportion of blueberry forest is increased in areas with low forest cover, whereas it is opposite in areas of high forest cover.

The density of power lines is identified as a factor affecting the black grouse density negatively, despite it was not included in the best-ranked models.

I further suggest that a positive relationship exists between pine marten and capercaillie, because the pine marten was identified by the modelling procedure, and the species showed a positive and significant correlation. However, many martens present in an area should not be interpreted as a cause of increased capercaillie density.

I finally reject the negative impact indicated by the modelling procedure on the black grouse density from an increase in proportion of remote areas. I do this because a possible methodical error was identified.

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References

ANGELSTAM, P., LINDSTROM, E. & WIDEN, P. 1984. Role of Predation in Short-Term Population Fluctuations of Some Birds and Mammals in Fennoscandia. *Oecologia,* 62**,** 199-208.

BAINES, D., MOSS, R. & DUGAN, D. 2004. Capercaillie breeding success in relation to forest habitat and predator abundance. *Journal of Applied Ecology,* 41**,** 59-71.

BAINES, D., WILSON, I. A. & BEELEY, G. 1996. Timing of breeding in black grouse Tetrao tetrix and capercaillie Tetrao urogallus and distribution of insect food for the chicks. *Ibis,* 138**,** 181-187.

BARNES, R. F. W. 1987. Long-Term Declines of Red Grouse in Scotland. *Journal of Applied Ecology,* 24**,** 735-741.

BEVANGER, K. 1995. Estimates and population consequences of tetraonid mortality caused by collisions with high tension power lines in Norway. *Journal of Applied Ecology,* 32**,** 745-753.

BOLLMANN, K., WEIBEL, P. & GRAF, R. F. 2005. An analysis of central Alpine capercaillie spring habitat at the forest stand scale. *Forest Ecology and Management,* 215**,** 307-318.

BOX, G. E. P. & JENKINS, G. M. 1970. *Time series analysis: forecasting and control,* San Francisco, Holden-Day.

BRAINERD, S., KASTDALEN, L., KÅLÅS, J. A., HOEM, S. A., ROLANDSEN, C. & PEDERSEN, H. C. 2005. *Locally-based management and national monitoring of small game. A summary of current knowledge with recommendations for future efforts. NINA Report 38.*

BRAINERD, S. M. & ROLSTAD, J. 2002. Habitat selection by Eurasian pine martens Martes martes in managed forests of southern boreal Scandinavia. *Wildlife Biology,* 8**,** 289-297.

BUCKLAND, S. T. & ANDERSON, D. R. 2001. *Introduction to distance sampling: estimating abundance of biological populations*, Oxford University Press.

BURNHAM, K. P. & ANDERSON, D. R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach,* New York, Springer.

FRAMSTAD, E. 2010. *Natur i endring: Terrestrisk naturovervåking i 2009: Markvegetasjon, smågnagere og fugl,* Trondheim, Norsk institutt for naturforskning (in Norwegian).

GEONORGE. 2011. *Find Interactive Maps, GIS datasets, Satellite Imagery and Related Applications* [Online]. Norwegian Mapping Authority / Norway Digital. Available: http://www.geonorge.no/geonetwork/srv/en/main.home [Accessed 20-03-2011].

GJERSHAUG, J. O. & NYGÅRD, T. 2003. Reports for the Large Predator Policy Statement. Golden Eagle in Norway: Population, predator role and management. *NINA fagrapport 58.* Trondheim: NINA.

GJERTSEN, A. K. 2007. Accuracy of forest mapping based on Landsat TM data and a kNN-based method. *Remote Sensing of Environment,* 110**,** 420-430.

GREGERSEN, F. & GREGERSEN, H. 2009. Ongoing population decline and range contraction in Norwegian forest grouse. *Ornis Norvegica,* 32**,** 179-189.

HAGEN, Y. 1952. *Rovfuglene og viltpleien,* Oslo, Gyldendal (in Norwegian).

HJELJORD, O. 2008. *Viltet : biologi og forvaltning,* Oslo, Tun forl (in Norwegian).

HORNFELDT, B., LOFGREN, O. & CARLSSON, B. G. 1986. Cycles in Voles and Small Game in Relation to Variations in Plant-Production Indexes in Northern Sweden. *Oecologia,* 68**,** 496-502.

HURLBERT, S. H. 1984. Pseudoreplication and the Design of Ecological Field Experiments. *Ecological Monographs,* 54**,** 187-211.

HÖRNELL-WILLEBRAND, M. 2005. Temporal and spatial dynamics of willow grouse Lagopus lagopus. [Doctoral thesis]. *Acta Universitatis agriculturae Sueciae*.

IUCN. 2010. *IUCN Red List of Threatened Species. Version 2010.4.* [Online]. International Union for Conservation of Nature. Available: http://www.iucnredlist.org/ [Accessed 18-03-2011].

JOHANSEN, B. E. 2009. *Vegetasjonskart for Norge basert på landsat TM/ETM+data.,* Tromsø, Norut Tromsø (in Norwegian).

KASTDALEN, L. 1992. *Skogshøns og jakt,* [Oslo], Norges bondelag (in Norwegian).

KURKI, S., HELLE, P., LINDEN, H. & NIKULA, A. 1997. Breeding success of black grouse and capercaillie in relation to mammalian predator densities on two spatial scales. *Oikos,* 79**,** 301-310.

KURKI, S., NIKULA, A., HELLE, P. & LINDEN, H. 1998. Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. *Journal of Animal Ecology,* 67**,** 874-886.

KURKI, S., NIKULA, A., HELLE, P. & LINDEN, H. 2000. Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology,* 81**,** 1985-1997.

KVASNES, M. A. J., STORAAS, T., PEDERSEN, H. C., BJORK, S. & NILSEN, E. B. 2010. Spatial dynamics of Norwegian tetraonid populations. *Ecological Research,* 25**,** 367-374.

LANDE, U. S. 2011a. Adult density and chick production of capercaillie and black grouse in relation to landscape characteristics. Manuscript.

LANDE, U. S. 2011b. *Grouse - Habitat relationships : monitoring, scale and management,* Uppsala, Department of Wildlife, Fish and Environmental Studies.

LUDWIG, T., STORCH, I. & GAERTNER, S. 2009. Large-scale land use change may explain bird species declines in semi-natural areas: the case of Black Grouse population collapse in Lower Saxony, Germany. *Journal of Ornithology,* 150**,** 871-882.

MOA, P. F., HAGEN, B. R., SAND, O. M., PEDERSEN, H. C. & SOLVANG, H. 2009. *Resultater og erfaringer etter bruk av Distance-metoden ved hønsefugltakseringer i Midt-Norge. Rypeforvaltningsprosjektet 2006-2011.,* Steinkjer, Høgskolen i Nord-Trøndelag (in Norwegian).

NORWAY DIGITAL. 2011. *Nedlasting av data for parter i Norge digitalt (in Norwegian).* [Online]. Norwegian Mapping Authority. Available: www.statkart.no/Norge_digitalt/Norsk/Metadata/Nedlasting_av_data/ [Accessed 20-03-2011] (in Norwegian).

PEDERSEN, H. C., ANDERSEN, O., CHRISTENSEN, H., KALTENBORN, B. P., MIDTLUND, F. K. & STORAAS, T. 2007. The user-initiated research project "Grouse Management 2006-2011". *Grouse News,* 33**,** 18-19.

PEDERSEN, H. C., STEEN, H., KASTDALEN, L., BROSETH, H., IMS, R. A., SVENDSEN, W. & YOCCOZ, N. G. 2004. Weak compensation of harvest despite strong density-dependent growth in willow ptarmigan. *Proceedings of the Royal Society of London Series B-Biological Sciences,* 271**,** 381-385.

R DEVELOPMENT CORE TEAM, R. D. C. 2010. R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing.* Vienna, Austria.

ROLSTAD, J. 1989. *Habitat and range use of capercaillie Tetrao urogallus L. in southcentral Scandinavian boreal forests : with special reference to the influence of modern forestry,* Ås, Department of Nature Conservation, Agricultural University of Norway.

SANDERCOCK, B. K., NILSEN, E. B., BROSETH, H. & PEDERSEN, H. C. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. *Journal of Animal Ecology,* 80**,** 244-258.

SAT-SKOG. 2011. *Nedlasting av kartdata - SAT-SKOG.* [Online]. The Norwegian Forest and Landscape Institute. Available: http://www.skogoglandskap.no/kart/SAT-SKOG [Accessed 08-02-2011] (in Norwegian).

SATVEG. 2010. *SatVeg (satelittvegetasjonskart)* [Online]. Norwegian Directorate for Nature Management. Available: http://www.dirnat.no/content/347/ [Accessed 08-02-2011].

SEISKARI, P. 1962. On the winter ecology of the capercaillie, Tetrao urogallus, and the black grouse, Lyrurus tetrix, in Finland. *Riistatieteellisia Julkaisuja,* 22**,** 3-119.

SELÅS, V. 2000. Population dynamics of capercaillie Tetrao urogallus in relation to bilberry Vaccinium myrtillus production in southern Norway. *Wildlife Biology,* 6**,** 1-11.

SELÅS, V., STEEN, O. F. & JOHNSEN, J. T. 2008. Goshawk breeding densities in relation to mature forest in southeastern Norway. *Forest Ecology and Management,* 256**,** 446-451.

SIMPSON, E. H. 1949. Measurement of Diversity. *Nature,* 163**,** 688-688.

SOLVANG, H., MOA, P. F., BREISJØBERG, J. I., STORAAS, T. & PEDERSEN, H. C. 2007. *Årsrapport for rypetaksering 2006 : rypeforvaltningsprosjektet 2006-2011,* Elverum, Høgskolen i Hedmark (in Norwegian).

SOLVANG, H., STORAAS, T., HAGEN, B. R. & PEDERSEN, H. C. 2009. *Rapport for skogsfugltaksering 2005-2008 : rypeforvaltningsprosjektet 2006-2011,* Elverum, Høgskolen i Hedmark (in Norwegian).

SSB. 2011. *Small game and roe deer hunting, 2009/2010.* [Online]. Statistics Norway. Available: http://www.ssb.no/srjakt_en/ [Accessed 15-03-2011].

STORCH, I. 1993. Patterns and strategies of winter habitat selection in alpine capercaillie. *Ecography,* 16**,** 351-359.

SWENSON, J. E. & ANGELSTAM, P. 1993. Habitat separation by sympatric forest grouse in Fennoscandia in relation to boreal forest succession. *Canadian Journal of Zoology,* 71**,** 1303-1310.

TAUGBØL, T. 2001. *Hyttebygging i Norge: en oppsummering og vurdering av ulike miljø- og samfunnsmessige effekter av hyttebygging i fjell- og skogtraktene i Sør-Norge,* Trondheim, Norsk institutt for naturforskning (in Norwegian).

THIEL, D., JENNI-EIERMANN, S., BRAUNISCH, V., PALME, R. & JENNI, L. 2008. Ski tourism affects habitat use and evokes a physiological stress response in capercaillie Tetrao urogallus: a new methodological approach. *Journal of Applied Ecology,* 45**,** 845-853.

WARREN, P., BAINES, D. & RICHARDSON, M. 2009. Mitigating against the impacts of human disturbance on black grouse Tetrao tetrix in northern England. *Folia Zoologica,* 58**,** 183-189.

WEGGE, P. & KASTDALEN, L. 2007. Pattern and causes of natural mortality of capercaille, Tetrao urogallus, chicks in a fragmented boreal forest. *Annales Zoologici Fennici,* 44**,** 141-151.

WEGGE, P. & KASTDALEN, L. 2008. Habitat and diet of young grouse broods: resource partitioning between Capercaillie (Tetrao urogallus) and Black Grouse (Tetrao tetrix) in boreal forests. *Journal of Ornithology,* 149**,** 237-244.

WEGGE, P. & STORAAS, T. 1990. Nest Loss in Capercaillie and Black Grouse in Relation to the Small Rodent Cycle in Southeast Norway. *Oecologia,* 82**,** 527-530.

WILLEBRAND, T. & HORNELL, M. 2001. Understanding the effects of harvesting willow ptarmigan Lagopus lagopus in Sweden. *Wildlife Biology,* 7**,** 205-212.

Appendix A

- *Management Areas and Grouse Population Surveys*

A-1. Detailed information on management areas.

County	Area Num	Management Area Name	Municipality	Estate type	Area Size [km²]
Nord-Trøndelag	1	Ogndalen	Steinkjer	2c - Public: mix of public owners	503,9
	2	Bangdalen	Namsos, Overhalla, Steinkjer, Namdalseid	3a - Mix private / public	513,2
Hedmark	3	Vestre Trysil	Trysil	1b - Private: landowner association	176,9
	4	Ljørdalen	Trysil	3a - Mix private / public	325,0
	5	Løiten Almenning	Løten	1d - Private: community-owned common land	159,9
	6	Nordre Elverum	Elverum	3a - Mix private / public	117,0
	7	Stange Almenning	Stange	1d - Private: community-owned common land	111,2
	8	Romedal Almenning	Stange	1d - Private: community-owned common land	225,9
	9	Vang Almenning	Hamar	1d - Private: community-owned common land	219,0
	10	Tørmoen	Kongsvinger	1b - Private: landowner association	11,9
	11	Rafjellet	Kongsvinger	1b - Private: landowner association	31,7
	12	Evenstadlia	Stor-Elvdal	1c - Private: no landowner association/unorganized	78,7
	13	Gløtvola	Engerdal	2b - Public: Crown lands	119,3
	14	RØ	Åmot	2a - Public: Statskog	254,0
	15	Stangeskovene	Eidskog, Nes, Aurskog-Høland	1a - Private: one owner	144,4
Akershus & Oslo	16	Råsjø skog	Nannestad, Nittedal, Lunner	1c - Private: no landowner association/unorganized	86,8
	17	Minneåsen	Hurdal	1c - Private: no landowner association/unorganized	33,1
	18	Oslomarka	Oslo, Nittedal	1a - Private: one owner	202,7
Aust-Agder	19	Gjerstadskogene	Gjerstad, Nissedal	2a - Public: Statskog	138,5

A-2. Results of line transects sampling of forest grouse in Norway, 2004 – 2010. The density estimates are calculated with a confidence interval of 90%.

Management Area	Year	Total length of sampled transects [meter]	Black grouse [birds / km²]			Capercaillie [birds / km²]		
			Density	CI low	CI high	Density	CI low	CI high
Ogndalen	-	-	-	-	-	-	-	-
	2007	173 100	2	1	3	3	2	5
	2008	185 837	2	1	3	1	0.5	1.5
	2009	189 204	3	2	5	0.2	0.1	0.4
	2010	147 210	2.5	1	5	1.2	0.5	3
Bangdalen	-	-	-	-	-	-	-	-
	2007	138 000	4	2	9	2	1	10
	2008	113 765	2	1	4	1	0.7	2.5
	2009	101 547	3	2	5	1.5	0.7	3
	2010	74 750	2	1	4	2	1	4
Vestre Trysil	-	-	-	-	-	-	-	-
	2008	80 868	8	4	10	10	8	13
	2009	82 300	6	4	9	8	5	13
	2010	72 450	11	7	17	10	6	16
Ljørdalen	-	-	-	-	-	-	-	-
	2005	60 850	3	1	8	1	1	2
	2006	62 500	3	1	8	2	1	5
	2007	62 500	5	3	10	7	4	11
	2008	56 415	5	3	9	10	6	15
	2009	59 400	4	3	7	3	2	7
	2010	60 600	8	5	13	10	6	15
Løiten Almenning	2004	62 610	2	1	3	2	1	4
	2005	47 930	3	2	6	1	0.5	2
	2006	71 310	5	3	8	2	1	3
	2007	55 890	11	7	16	5	1	20
	2008	73 310	7	5	10	4	2	6
	2009	73 310	5	3	8	6	3	12
	2010	68 780	5	3	8	3	2	5
Nordre Elverum	2004	47 047	9	5	19	8	4	16
	2005	95 270	6	4	9	2	1	4
	2006	79 652	7	4	12	4	2	6
	2007	73 619	17	11	26	6	4	9
	2008	81 739	14	8	25	5	3	8
	2009	67 990	12	8	19	8	5	13
	2010	61 000	15	10	23	6	4	10

Management Area	Year	Total length of sampled transects [meter]	Black grouse [birds / km^2]			Capercaillie [birds / km^2]		
			Density	CI low	CI high	Density	CI low	CI high
Stange Almenning	2004	56 420	7	4	14	5	3	9
	2005	56 900	4	3	7	2	1	3
	2006	68 405	9	-	15	8	5	14
	2007	60 375	8	5	13	12	7	18
	2008	67 750	11	7	5	9	6	13
	2009	66 840	6	4	10	5	3	8
	2010	64 970	8	5	12	7	5	12
Romedal Almenning	-	-	-	-	-	-	-	-
	2006	37 850	13	6	30	5	2	16
	2007	28 400	8	4	15	6	3	11
	2008	36 450	4	2	6	3	1	8
	2009	36 228	3	1	6	3	1	7
	2010	27 750	2	1	4	7	3	18
Vang Almenning	2004	132 535	1.3	0.8	2.3	1.5	0.9	2.3
	2005	134 900	2	1	3	3	2	4
	2006	100 000	4	2	6	4	3	5
	2007	114 902	6	3	9	9	6	13
	2008	146 519	6	5	9	4	3	5
	2009	138 008	6	5	9	5	3	8
	2010	136 530	10	8	14	16	11	24
Tørmoen	-	-	-	-	-	-	-	-
	2006	31 900	6	2	18	8	4	15
	2007	34 090	2	1	4	3	2	7
	2008	31 000	5	2	12	4	2	8
	2009	27 300	2	1	11	1	0.4	2
	2010	-	-			-		
Rafjellet	2004	30 900	2	1	7	4	2	8
	2005	-	-	-	-	-	-	-
	2006	31 400	2	1	5	9	4	21
	2007	33 370	4	2	8	6	4	11
	2008	33 020	7	4	11	3	1	6
	2009	26 940	2	1	5	7	4	12
	2010	32 710	7	4	13	5	2	9
Evenstadlia	-	-	-	-	-	-	-	-
	2005	28 771	5	1	22	6	3	11
	2006	28 583	12	6	22	14	8	25
	2007	26 876	9	5	17	11	7	17
	-	-	-	-	-	-	-	-
	2010	37 457	5	3	10	6	4	9

Management Area	Year	Total length of sampled transects [meter]	Black grouse [birds / km²]			Capercaillie [birds / km²]		
			Density	CI low	CI high	Density	CI low	CI high
Gløtvola	-	-	-	-	-	-	-	-
	2007	79 200	2	1	3	3	2	5
	2008	65 810	3	1	5	0.5	0.3	1.3
	-	-	-	-	-	-	-	-
	2010	59 600	-	-	-	5	2	10
RØ	2004	-	-	-	-	-	-	-
	2005	100 902	3	2	6	2	1	3
	-	-	-	-	-	-	-	-
Stange-skovene	-	-	-	-	-	-	-	-
	2009	73 820	8	6	12	7	4	13
	2010	85 850	10	7	15	4	3	6
Råsjø skog	-	-	-	-	-	-	-	-
	2007	44 620	18	11	31	4	2	1
	2008	47 520	5	3	9	2	1	3
	2009	49 820	5	3	9	3	2	7
	2010	46 680	9	6	15	5	2	10
Minneåsen	-	-	-	-	-	-	-	-
	2007	30 650	5	2	9	7	3	18
	2008	35 930	5	3	10	4	1	12
	2009	30 240	10	4	21	5	2	16
	2010	33 090	8	8	14	-	-	-
Oslomarka	2004	89 052	5	3	9	2	2	4
	2005	168 366	3	2	5	3	1	5
	2006	100 000	4	3	7	2	1	4
	-	-	-	-	-	-	-	-
	2009	111 728	3	2	6	4	2	7
	2010	79 469	12	8	18	2	0.7	3
Gjerstad-skogene	2004	80 336	7	4	14	-	-	-
	2005	44 113	10	6	18	-	-	-
	2006	91 104	12	8	18	-	-	-
	2007	58 319	11	8	18	2	1	8
	2008	71 436	14	8	24	-	-	-
	2009	69 400	17	11	25	1	1	3
	2010	70 305	19	13	28	6	3	11

Appendix B

- *Variable Definitions*

B-1. Identified variables used in the procedure of information collection.

Variable Category	Type of variable	Variable specification
Landscape	1. Habitat quality (Landscape types and vegetation structure)	a) Average size of forest stands. b) Productivity: Proportion of forest producing > 3 m^3 / ha per year. c) Percentage of old forest (age > 80 years). d) Landscape heterogeneity (SiD – Simpson's index of Diversity)
	2. Interference (accessibility and disturbance)	a) Proportion of remote areas: part of a management area > 0.3, 1, and 3 km from roads / cabins / settlement areas, respectively. b) Density of buildings in a management area. c) Power line density. Length of power lines / the management area size (if possible, grade on size / line capacity).
Predation	3. Population of predators	Density index of predator species: Red fox (*Vulpes vulpes*). Marten (*Martes martes*). Golden Eagle (*Aquila chrysaetos*). Goshawk (*Accipiter gentilis*).
	4. Population of small rodents	Small rodent density index
Management and hunting	5. Forest grouse protection	Share of refuges within a management area. Protection of female birds.
	6. Hunting regulation	Hunting licenses regime (Seasonal, short term, sale of quotas, exclusive rent, all) Bag limit. Hunting limitations in time?
	7. Harvest rate	Hunting bag or proportion harvested in relation to the estimated annual densities.
	8. Management area	Type of management area, e.g. public / private / community-owned common land. Size of management area.

B-2. Variable acronyms used in model selections.

Variable	Variable description	Measuring unit
A1km	Proportion of areas > 1 km away from roads and buildings.	[%]
AreaSize	Size of management area in km^2.	[km^2]
AreaType	Type of management area, i.e., private, public or mix of landowners.	Private / public / mix
BForest	Proportion of areas defined as blueberry forest within a management area.	[%]
Bogs	Proportion of areas defined as bogs within a management area.	[%]
DensB	Density of buildings within a management area.	[buildings / km^2]
DensBG	Population density of black grouse.	[birds / km^2]
DensCA	Population density of capercaillie.	[birds / km^2]
DensP	Density of power lines within a management area.	[km lines / km^2]
ForestC	Proportion of areas defined as forest of any type within a management area.	[%]
Fox	Density index of foxes.	[# intersections / km]
Marten	Density index of martens.	[# intersections / km]
OldF	Proportion of areas defined as old forest within a management area. Old forest defined as forest older than 80 years.	[%]
Prod	Productivity: proportion of medium or high productivity class within a management area.	[%]
SiD	Simpson Index of Diversity as a measurement of landscape heterogeneity.	Range: [-1, 1]
Stands	Mean size of forest stands within a management area.	[decare]
WType	Dominant wood type within the management area. Only pine and spruce relevant for the management areas contained in this study.	Pine / Spruce

Appendix C

- Details of Statistical Analysis

C-1. Correlation of habitat quality variables used as input to the PCA-procedure carried out prior to the model selection. Highly correlated variables (significant) are in bold.

Habitat quality variables.	**Stands**	**Productivity**	Old forest	Wood Type (Pine --> Spruce)	SiD - landscape heterogeneity	Blueberry forest	**Bogs**	**Forest cover**
Stands	1.00	**0.79**	- 0.14	0.34	0.31	0.12	- 0.55	**0.78**
Productivity	**0.79**	1.00	- 0.45	0.56	0.24	0.05	**- 0.67**	**0.80**
Old forest	- 0.14	- 0.45	1.00	- 0.57	0.22	- 0.46	0.13	- 0.02
Wood type (Pine => Spruce)	0.34	0.56	- 0.57	1.00	- 0.30	0.12	0.00	0.12
SiD - landscape heterogeneity	0.31	0.24	0.22	- 0.30	1.00	- 0.50	- 0.18	0.29
Blueberry forest	0.12	0.05	- 0.46	0.12	- 0.50	1.00	- 0.23	0.06
Bogs	- 0.55	**- 0.67**	0.13	0.00	- 0.18	- 0.23	1.00	**- 0.84**
Forest cover	**0.78**	**0.80**	- 0.02	0.12	0.29	0.06	**- 0.84**	1.00

C-2. Correlation of selected variables used as input to the PCA-procedure carried out prior to the final model selection. Highly correlated variables (significant) are in bold.

Selected variables for final analysis	Wood Type (Pine => Spruce)	SiD - landscape heterogeneity	Blueberry forest	**Forest cover**	**Proportion of remote areas**	Density power lines	**Man. Area Size**	Fox	Marten
Wood type (Pine => Spruce)	1.00	- 0.49	0.47	0.05	- 0.45	0.00	- 0.05	0.17	- 0.25
SiD - landscape heterogeneity	- 0.49	1.00	- 0.62	0.35	- 0.17	0.26	- 0.31	0.11	0.13
Blueberry forest	0.47	- 0.62	1.00	- 0.10	- 0.08	0.19	0.01	0.21	- 0.43
Forest cover (CA only)	0.05	0.35	- 0.10	1.00	**- 0.85**	0.31	**- 0.72**	0.43	0.06
Proportion of remote areas	- 0.45	- 0.17	- 0.08	**- 0.85**	1.00	- 0.24	**0.76**	- 0.49	0.02
Density Power lines	0.00	0.26	0.19	0.31	- 0.24	1.00	- 0.30	0.06	- 0.13
Management Area Size	- 0.05	- 0.31	0.01	**- 0.72**	**0.76**	- 0.30	1.00	- 0.31	0.00
Fox	0.17	0.11	0.21	0.43	- 0.49	0.06	- 0.31	1.00	0.08
Marten	- 0.25	0.13	- 0.43	0.06	0.02	- 0.13	0.00	0.08	1.00

C-3. Detailed model selection table. Models ranked according to ΔAICc-values. The selected model in each variable category in bold.

Step 1 - Habitat quality analysis:							
Species	**Rank**	**Fixed factors of LME-model**	**AICc**	**ΔAICc**	Coefficient	**Estimate**	**SE**
Black grouse	**1**	**WType * SiD**	**148.60**	**-**	(Intercept)	5.97	1.35
					WTypeSpruce	- 5.32	1.40
					SiD	- 7.20	2.22
					WTypeSpruce:SiD	9.03	2.33
	2	WType * OldF + SiD	150.10	1.50	(Intercept)	3.36	0.73
					SiD	1.83	0.68
					WTypeSpruce	- 2.82	0.79
					OldF	- 0.08	0.02
					WTypeSpruce:OldF	0.09	0.03
	3	WType * SiD + PCA-score	150.69	2.09	-	-	-
Capercaillie	**1**	**BForest * ForestC**	**182.48**	**-**	(Intercept)	- 6.40	2.09
					ForestC	0.10	0.03
					BForest	0.69	0.24
					ForestC:BForest	- 0.01	0.003
	2	BForest * ForestC + WType	182.60	0.12	(Intercept)	- 6.52	1.96
					WType	0.36	0.24
					ForestC	0.10	0.03
					BForest	0.67	0.23
					ForestC:BForest	- 0.01	0.003
	3	BForest * ForestC + OldF	182.77	0.29	(Intercept)	- 6.46	1.98
					OldF	- 0.02	0.01
					ForestC	0.11	0.03
					BForest	0.73	0.23
					ForestC:BForest	- 0.01	0.003
	4	BForest * ForestC + SiD	184.12	1.64	(Intercept)	- 5.92	2.18
					SiD	- 0.61	0.86
					ForestC	0.10	0.03
					BForest	0.65	0.25
					ForestC:BForest	- 0.01	0.003
	5	BForest * PCA-score	187.86	5.38	-	-	-

Step 2 - Interference analysis:							
Species	**Rank**	**Fixed factors of LME-model**	**AICc**	**ΔAICc**	Coefficient	**Estimate**	**SE**
Black grouse	**1**	**A1km * DensP**	**141.96**	**-**	(Intercept)	1.83	0.30
					A1km	0.02	0.01
					DensP	0.05	1.25
					A1km:DensP	- 0.29	0.10
	2	A1km * DensP + DensB	143.74	1.78	(Intercept)	1.90	0.32
					DensB	- 0.03	0.05
					DensP	- 0.03	1.25
					A1km	0.02	0.01
					A1km:DensP	- 0.28	0.10
	3	A1km	145.75	3.79	-	-	-
Capercaillie	1	A1km + DensP	171.76	-	(Intercept)	2.09	0.32
					A1km	- 0.03	0.01
					DensP	- 2.01	1.23
	2	**A1km**	**172.21**	**0.46**	(Intercept)	1.68	0.21
					A1km	- 0.03	0.01
	3	A1km + DensP + DensB	173.17	1.41	(Intercept)	2.19	0.33
					A1km	- 0.03	0.01
					DensB	- 0.05	0.05
					DensP	- 2.06	1.20
	4	A1km + DensP * DensB	173.69	1.93	(Intercept)	1.66	0.53
					A1km	- 0.03	0.01
					DensB	0.27	0.25
					DensP	1.88	3.33
					DensB:DensP	- 2.46	1.96
	5	A1km * DensP	173.72	1.96	(Intercept)	2.06	0.34
					A1km	- 0.03	0.02
					DensP	- 1.88	1.39
					A1km:DensP	- 0.02	0.12
	6	A1km + DensB	173.80	2.04	-	-	-

Step 3 - Predator analysis:							
Species	**Rank**	**Fixed factors of LME-model**	**AICc**	**ΔAICc**	Coefficient	**Estimate**	**SE**
Black grouse	**1**	**1 (i.e., intercept only)**	**119.87**	**-**	(Intercept)	1.59	0.15
	2	Marten	121.49	1.62	(Intercept)	1.53	0.20
					Marten	- 0.31	0.42
	3	Fox	121.81	1.94	(Intercept)	1.51	0.22
					Fox	- 0.03	0.09
	4	Fox + Marten	123.62	3.75	-	-	-
Capercaillie	**1**	**Marten**	**153.52**	**-**	(Intercept)	0.94	0.24
					Marten	1.30	0.52
	2	Fox + Marten	155.47	1.95	(Intercept)	1.01	0.28
					Fox	- 0.06	0.13
					Marten	1.41	0.58
	3	1 (i.e., intercept only)	157.11	3.59	-	-	-
Step 4 - Management analysis:							
Species	**Rank**	**Fixed factors of LME-model**	**AICc**	**ΔAICc**	Coefficient	**Estimate**	**SE**
Black grouse	**1**	**AreaSize**	**152.28**	**-**	(Intercept)	1.909	0.196
					AreaSize	- 0.002	0.001
	2	AreaSize * AreaType	154.50	2.22	-	-	-
Capercaillie	**1**	**AreaSize + AreaType**	**178.51**	**-**	(Intercept)	1.784	0.305
					AreaSize	- 0.002	0.001
					AreaTypePrivate	- 0.053	0.499
					AreaTypePublic	- 0.873	0.283
	2	AreaSize * AreaType	180.22	1.71	(Intercept)	2.118	0.394
					AreaSize	- 0.003	0.001
					AreaTypePrivate	- 0.589	0.426
					AreaTypePublic	- 1.207	0.534
					AreaSize: AreaTypePrivate	0.003	0.002
					AreaSize: AreaTypePublic	0.001	0.002
	3	AreaType	182.74	4.23	-	-	-

Step 5 - All categories analysis:							
Species	**Rank**	**Fixed factors of LME-model**	**AICc**	**ΔAICc**	Coefficient	**Estimate**	**SE**
Black grouse	1	WType * SiD + AreaSize	116.46	-	(Intercept)	5.619	2.338
					AreaSize	- 0.001	0.001
					WTypeSpruce	- 4.814	2.298
					SiD	- 6.332	3.481
					WTypeSpruce:SiD	8.268	3.497
	2	**A1km**	**117.14**	**0.69**	(Intercept)	1.774	0.200
					A1km	- 0.017	0.007
	3	WType * SiD	117.25	0.79	(Intercept)	4.250	2.412
					WTypeSpruce	- 3.911	2.445
					SiD	- 4.699	3.646
					WTypeSpruce:SiD	7.106	3.732
	4	PCA-score	117.56	1.11	(Intercept)	1.490	0.149
					PCA-score	- 0.186	0.082
	5	WType * SiD + PCA-score	117.70	1.24	(Intercept)	4.736	2.337
					PCA-score	- 0.105	0.078
					WTypeSpruce	- 4.136	2.346
					SiD	- 5.256	3.522
					WTypeSpruce:SiD	7.131	3.579
	6	WType * PCA-score + SiD	117.70	1.24	(Intercept)	- 1.625	1.155
					SiD	1.874	0.855
					WTypeSpruce	2.225	0.933
					PCA-score	1.328	0.724
					WTypeSpruce:PCA-score	- 1.434	0.720
	7	SiD * PCA-score + DensP	117.88	1.42	(Intercept)	0.977	0.409
					DensP	- 2.270	1.272
					SiD	1.516	0.741
					PCA-score	0.452	0.320
					SiD:PCA-score	- 1.408	0.696
	8	WType * DensP + SiD	118.46	2.00	-	-	-

Step 5 - All categories analysis:							
Species	**Rank**	**Fixed factors of LME-model**	**AICc**	**ΔAICc**	Coefficient	**Estimate**	**SE**
Capercaillie	**1**	**PCA-score * BForest + Marten**	**130.12**	**-**	(Intercept)	1.111	0.309
					Marten	1.636	0.398
					PCA-score	1.115	0.183
					BForest	- 0.028	0.031
					PCA-score:BForest	- 0.114	0.023
	2	PCA-score * BForest + Marten + Fox	130.91	0.78	(Intercept)	1.143	0.304
					Marten	1.861	0.437
					Fox	- 0.134	0.107
					PCA-score	1.080	0.184
					BForest	- 0.008	0.0.35
					PCA-score:BForest	- 0.107	0.024
	3	PCA-score*BForest + Marten + WType	132.34	2.21	-	-	-